Characteristics of fish communities in coastal waters of north-western Australia, including the biology of the threadfin species *Eleutheronema tetradactylum* and *Polydactylus macrochir*

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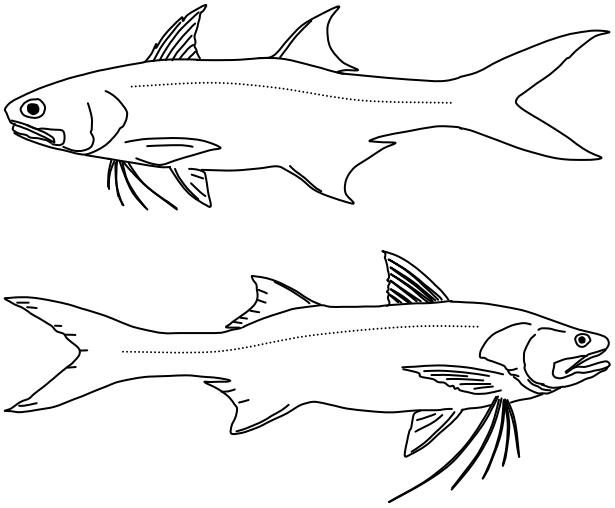

I declare that this thesis is my own account of my research and contains as its main content, work which has not previously been submitted for a degree at any University

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2006

Joe Hunter and family with a feed of Blue Salmon – Broome, 1979 R. Garwood

Abstract

This study was aimed at determining the characteristics of the fish assemblages in nearshore coastal waters of the remote Canning region of tropical Western Australia and to obtain sound quantitative data on crucial aspects of the biology of the two threadfin species, which are commercially and recreationally important in those waters. The community studies focused on comparing the species compositions of the fish faunas found over bare sand and in mangroves and rock pools and on elucidating the factors that influence those compositions. The population studies concentrated on exploring the hermaphroditic characteristics, size and age structures, growth and stock status of the two species of Polynemidae.

The arid Canning coast of north-western Australia, which lies between Cape Leveuque (16°21′ S, 123°02′ E) and Cape Keraudren (19°57′ S, 119°46′ E), does not contain rivers and thus also estuaries, which traditionally provide alternative fish nursery areas to those found in nearshore waters. It is also subjected to some of the largest tides in the world. The fish faunas at three widely-separated locations, *i.e*. Port Smith, Eighty Mile Beach and Cape Keraudren, were sampled using seine and gill netting in their shallow, nearshore waters and rotenoning in intertidal pools at the first and third of those locations with the aim of determining the following. 1) The extents to which the diversity, abundance and species composition of the fish faunas of the Canning coast are influenced by location, habitat and time of year. 2) Which species use bare sand, mangroves and/or intertidal pools as nursery areas and which are permanent residents in one or more of those habitats. 3) Identification of the commercial and recreational fish species found in each of the above three habitat types and their relative abundance in those habitats.

The fish catches from all three sampling locations collectively yielded 170 species representing 66 families. The most abundant species (with % contributions) in seine net samples collected over unvegetated sand were *Stolephorus carpentariae* (19.1), *Herklotsichthys blackburni* (14.7) and *Atherinomorus lacunosus* (11.8), whereas those in gill net samples taken over the same substrate were *Arius proximus* (26.6), *Eleutheronema tetradactylum* (18.8) and *Polydactylus macrochir* (18.7) and in mangroves were *A. proximus* (38.9), *Valamugil buchanani* (18.8) and *Scomberoides commersonnianus*

(18.7). *Ambassis vachellii* (32.5) and *Craterocephalus capreoli* (14.4) dominated the catches obtained from intertidal pools.

Fifty three of the 170 species that were caught are fished commercially and recreationally along the Canning coast and a further 17 fish species are caught solely by recreational fishers. The most abundant of these species were the polynemids *E. tetradactylum* and *P. macrochir*, which are residents of nearshore waters, *i.e.* are found in these waters throughout the whole of their life cycle. Other species, such as *Lutjanus russelli Epinephelus coioides* and *Sillago vittata,* are present in nearshore waters only as juveniles and thus use these waters as a nursery.

The compositions of the ichthyofaunal samples collected by both seine and gill nets over bare sand differed markedly among locations. The compositions at Cape Keraudren, the most southerly location, were more similar to those at Port Smith, the most northerly and most protected location, than those that Eighty Mile Beach, the most exposed of the three locations. It is thus proposed that the compositions of the fish faunas found in nearshore, unvegetated waters along the Canning coast are influenced more by factors related to turbidity than those reflecting latitudinal position. The fish fauna at Eighty Mile Beach was distinguished by species typically associated with turbid waters, such as those of the Polynemidae and Sciaenidae and certain species of the Engraulidae, Ariidae, Mugilidae and Carcharhinidae. In contrast, many of those species were absent from catches made in the clearer waters of Port Smith, where the ichthyofauna was disitinguished by certain species of the Clupeidae and Atherinidae and other species associated with low turbidity, such as *V. buchanani* and *Chanos chanos*.

The compositions of the fish faunas sampled over bare sand by gill and seine nets underwent marked seasonal changes. Furthermore, these changes, particularly in the case of seine net catches, tended to undergo a conspicuous cyclical progression during the year as a result of time-staggered changes in the recruitment and emigration of certain species. The species responsible for seasonal differences in either the gill and/or seine net samples included nearshore residents, such as the clupeids *H. blackburni* and *Spratelloides delicatulus,* the polynemids *E. tetradactylum* and *P. macrochir*, the engraulidid *Thryssa hamiltonii* and the atherinids *A. lacunosus* and *C. capreoli*, as well as species such as the sillaginid *S. vittata*, which use nearshore waters as a nursery area. At a broader level, the compositions of the fish sampled by gill net in the wet and dry periods were also distinct,

reflecting, in particular, the influx of certain species during the wet period, *e.g*. mature ariid catfish and the juveniles of a number of elasmobranchs, such as the endangered Green Sawfish *Pristis zijsron*, aggregate in nearshore, shallow waters during this period.

The fish faunas of the intertidal pools at Port Smith and Cape Keraudren, which were sampled using rotenone, differed markedly from each other and from those over nearby bare sand substrates on the coast. The ichthyofauna of intertidal pools at Port Smith was distinguished from that at Cape Keraudren by relatively greater numbers of *C. capreoli* at the former location, whereas the opposite situation pertained with *Amniataba caudavittatus, Acanthopagrus latus* and *L. macrolepis* at Cape Keraudren. These differences were attributable to differences in habitat characteristics of intertidal pools, with pools at the former location containing clearer water and greater amounts of rock, while those at the latter contained mangroves. Few species were caught in both intertidal pools and in the surrounding shallow, nearshore waters, demonstrating that the rock pools provide an important habitat for certain fish species.

The composition of the fish fauna of intertidal pools at Port Smith underwent an essentially cyclical progression over the course of a year, reflecting the timing and strength of recruitment of the juveniles of the various species. The species responsible for this recruitment-related change in the fish fauna included both nearshore residents, such as *A. vachellii, C. capreoli* and *A. lacunosus*, as well as transient species that use intertidal pools as a nursery area, *i.e. E. coioides* and *L. russelli*. In contrast, the seasonal progression in species composition in intertidal pools at Cape Keraudren was largely related to the influence of a tropical cyclone. The fish community in the period immediately following the cyclone was depauparate and distinguished, from that before the cyclone, in particular by a lack of *A. vachellii* and *A. latus*.

The Blue and King Threadfins *E. tetradactylum* and *P. macrochir*, which were among the most abundant species in the seine and gill net catches taken in unvegetated waters, are key species in the Kimberley Managed Gill Net and Barramundi Fishery (KMGBF) and important recreational target species. In addition, these species are an important source of food and of cultural significance for local indigenous communities. The importance of the shared nature of these resources and the marked fluctuations undergone by the catches of threadfin in recent years led to the second major component of this thesis, *i.e.* to obtain reliable data on the reproductive biology, age compositions,

growth rates and mortality of *E. tetradactylum* and *P. macrochir,* of the type that are required by managers for developing plans to conserve the stocks of these species in north-western Australia.

Length and age compositions of male, bisexual (*i.e.* possessing gonads comprising both testicular and ovarian tissue) and female *E. tetradactylum* and *P. macrochir*, and histological characteristics of the gonads of the full size range of threadfin were examined and analysed. The results demonstrate that, in north-western Australian waters, each of these species is a protandrous hermaphrodite, *i.e*. individuals mature first as males before changing sex to female. Sexual maturity is attained by 50% of male *E. tetradactylum* and *P. macrochir* at *ca* 200 and 230 mm, respectively. For both species, these lengths approximate those attained towards the end of their first year of life. However, the lengths and ages at which these two species typically change sex differ markedly.

In the case of *E. tetradactylum*, "transitional" fish (*i.e.* those with bisexual gonads assumed to be changing sex) were most prevalent at total lengths between 300 and 400 mm. All fish greater than 450 mm total length possessed gonads that consisted exclusively of ovarian tissue. The L_{50} for sex change from male and transitional fish to females is *ca* 400 mm. Thus, the majority of *E. tetradactylum* change sex during their second or third years of life and males are rarely older than three years. In contrast, the range of lengths at which transitional individuals of *P. macrochir* were recorded was much broader than *E. tetradactylum*, *i.e.* between 310 and 1140 mm. The data on the prevalences of males and females in sequential age classes demonstrate that sex change can occur in *P. macrochir* as young as two years old and up to eight years old. The lengths at which *E. tetradactylum* changes sex in north-western Australia was relatively similar at all locations, whereas the L_{50} for sex change in *P. macrochir* varied markedly among sampling locations. For example, the L_{50} value for sex inversion was *ca* 790 mm at Derby, compared with *ca* 1160 mm at Anna Plains. The differences presumably reflect variations in environmental conditions at those localities.

Analysis of the ages of male, transitional and female *E. tetradactylum* revealed that the change from male to female by this species occurs over a period of *ca* 6 months. The presence of mature sperm in transitional gonads, in combination with trends exhibited by the GSIs of the testicular and ovarian portions of transitional gonads, demonstrate that, during the spawning season, transitional threadfin function as males. Analyses indicate

that, once individual *E. tetradactylum* and *P. macrochir* change sex to become females, all individuals function as mature females during successive breeding seasons. Both species of threadfin have protracted spawning periods of *ca* 6 months. However, the monthly trends exhibited by the mean GSIs and the proportion of the various gonad stages show that the spawning of both species peaks during spring and early summer, *i.e.* September to December, and occurs on multiple occasions each year.

In north-western Australia, *P. macrochir* grows far larger and lives for longer than *E. tetradactylum*, a difference reflected in the maximum total lengths and ages recorded for these two species, *i.e.* 1393 mm and 10 years *vs* 793 mm and 6 years, respectively. In addition, *P. macrochir* grows faster than *E. tetradactylum*, attaining lengths of 322, 520 and 945 mm *vs* 245, 400 and 635 mm, by the end of years 1, 2 and 5, respectively. For both species, estimates of total, natural and fishing mortality were derived using different life history models, simulation based on the number of fish in samples above a specified age, relative abundance analyses and a Monte Carlo resampling approach.

The various biological parameters determined for *E. tetradactylum* and *P. macrochir*, including the estimates of mortality, were incorporated into yield per recruit, spawning biomass per recruit and spawning potential ratio analyses to determine the current impacts of fishing on each species in north-western Australia. The results of these analyses indicate that *E. tetradactylum* is fully exploited and that *P. macrochir* is overexploited. The effectiveness of various management options is evaluated.

The data produced during the first part of this thesis on the diversity, abundance and species compositions of fish faunas in different nearshore habitats along the Canning coast of north-western Australia, and the way these faunas are influenced by season, provides fisheries and environmental managers with information that will enable them to develop management plans for these habitats and their fish species. In addition, the biological data for *E. tetradactylum* and *P. macrochir*, and the results of the stock assessments performed on these species, will enable fisheries managers to develop plans for conserving the stocks of these two species in north-western Australia.

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1. General Introduction

1.1. Fish faunas of nearshore tropical waters

Fish are by far the most diverse of all vertebrate groups, with the number of their recognised species exceeding 25 000 and continuing to increase as new species are described (Eschmeyer & Froese, 2003; O'Dor, 2003). The diversity of fishes is highest in the tropics, where, in marine waters, it is greatest in the shallow waters of continental shelves (Nelson, 1994). The importance of the contribution made by the fishes found in tropical shelf waters to the diversity of fishes in general is emphasised by the fact that, while only *ca* 30% of the worlds continental shelf area is located in the tropics (Longhurst & Pauly, 1987), this area alone accounts for almost 70% of all marine and estuarine fish species (Lowe-McConnell, 1987; O'Dor, 2003).

The diversity of tropical fish species is typically greatest in structurally-complex coral reef habitats (Emery, 1978; Ohman & Rajasuriya, 1998; Gratwicke & Speight, 2005). Because of the important role played by coral reefs in sustaining the diversity of fish in the Indo-West Pacific, the fish faunas of that habitat type have been particularly well studied in this region (e.g. Bellwood & Wainwright, 2002). It is important to recognise, however, that, as coral reefs are found only in relatively clear waters, that type of habitat represents only a small part of the continuum of habitats found in shallow water along tropical coastlines (Longhurst & Pauly, 1987).

Seagrass meadows also constitute highly productive shallow water ecosystems and consequently act as important habitats for certain marine fish (Coles *et al*., 1993; Nagelkerken *et al*., 2001, 2002, Heck *et al*., 2003; Dorenbosch *et al*., 2005a). The fish communities inhabiting seagrass meadows are typically distinct from those found in other nearby habitats (Robertson & Duke, 1987; Blaber *et al*., 1992, Chittaro *et al*., 2005) and the presence of seagrass in nearshore waters has a marked influence on the total diversity of fish found in those waters (Blaber *et al*., 1994; Dorenbosch *et al*., 2005b; Lugendo *et al*., 2005). However, seagrass meadows, like coral reefs, are typically found only in those parts of the coastline that are neither turbid nor exposed to very large tidal water movements.

Estuaries in the tropics are highly productive ecosystems and consequently house relatively diverse fish assemblages (Hatcher *et al*., 1989; Robertson & Blaber, 1992; Blaber, 2000). Although approximately half of the fish species found in tropical estuaries are able to complete their life cycles within those systems (Longhurst & Pauly, 1987; Blaber *et al*., 1989, 1994), these estuaries also provide important habitats for a number of fish species that spawn in marine waters. Blaber & Blaber (1980) demonstrated that nearshore, shallow waters with estuarine-like conditions, such as high turbidity, act as a nursery area for the juveniles of a range of tropical fish species. Thus, where estuaries are absent along arid coastlines in the tropics, those shallow, nearshore waters of that coastline which possess estuarine-like characteristics presumably constitute particularly important nursery areas for some species that might otherwise have entered estuaries as juveniles.

Mangroves, which are often found in tropical estuaries, are highly productive ecosystems (Robertson *et al*., 1992; Blaber, 2000). Consequently, mangroves provide an important habitat for fish, providing both an abundance of food and shelter from predation (Laegdsgaard & Johnson, 1995; Cocheret de la Morinière *et al*., 2004). The structural complexity of mangrove stands, in combination with the range of potential food they contain, accounts for the diversity of the fish assemblages found in this type of habitat (Sasekumar *et al*., 1992; Rönnbäck *et al*., 1999; Laegdsgaard & Johnson, 2001; Lugendo *et al*., 2006). Although mangroves are mostly found in estuaries, they are also present along the coastline and, as with mangroves in estuaries, have been shown to constitute important habitats for many fish species (Nagelkerken *et al*., 2000b; Cocheret de la Morinière *et al*., 2002; Nagelkerken & van der Velde, 2002). Indeed, such mangroves may play an essential nursery role for species such as the threatened Caribbean parrotfish *Scarus guacamaia* (Mumby *et al*., 2004; Dorenbosch *et al*., 2006).

Although mangroves constitute important habitats in estuaries and along nearshore tropical coastal areas, the nearshore waters along these coastlines also have unvegetated substrates which are inhabited by fish communities that are distinct from mangroves (Blaber *et al*., 1985). Although the fish fauna of unvegetated waters is typically dominated by small pelagic resident species, such as members of the Clupeidae or Engraulidae (e.g. Black *et al*., 1990; Ikejima *et al*., 2003), which complete their life cycle in nearshore waters, this habitat also constitutes an important nursery area for the juveniles of some

other species, such as sillaginids, cynoglossids and bothids (Weng, 1983; van der Veer *et al*., 1994).

Intertidal pools constitute important habitats in nearshore waters, particularly in those areas that are characterised by considerable tidal movements and consequently have a particularly wide intertidal zone, as they constitute the only habitat available to fish in these areas during low tide (Gibson, 1999, 2003). A considerable proportion of the fish inhabiting intertidal pools complete their life cycle in such pools and are thus permanent residents of that type of habitat (Gibson, 1982; Pfister, 1996; Prochazka, 1996; Almada & Faria, 2004). In contrast, the remainder of the ichthyofauna inhabiting intertidal pools are transient visitors to this habitat, a component of which use this habitat as a nursery area whilst juveniles (Pfister, 1999).

The various environmental characteristics of intertidal pools, including salinity, temperature and dissolved oxygen, frequently vary markedly over a tidal cycle. Members of particularly the Gobiidae and Blenniidae are adapted morphologically and/or behaviourally to this variable environment, through possessing, for example, the ability to respire cutaneously or emerge from hypoxic water (Evans *et al*., 1999; Martin & Bridges, 1999). Transient visitors, which lack these types of adaptation, are thus less likely to be successful in intertidal pools (Bridges, 1993).

The habitat work in this PhD thesis has concentrated on quantitatively describing and comparing the characteristics of the ichthyofaunas in nearshore unvegetated areas, intertidal pools and coastal mangroves in an isolated region of north-western Australia.

1.2. The north-western Australian coast and its fish fauna

The coast of Western Australia, which extends for 20 000 km and encompasses more than 21° in latitude, exhibits a continuum of climatic conditions from warm monsoonal in the tropical far north to temperate on the south coast. These vast differences in climatic conditions, together with those in geomorphology and tidal regimes, account for the extraordinary diversity of the marine fauna and flora of nearshore waters of this coastline as a whole (Semeniuk, 1983, 1985; Hutchins, 1991, 1994, 2001b; Ayvazian & Hyndes, 1995). On the basis of climate, tidal regime, hydrology and geomorphology, north-western

Australia has been separated into three main bioregions, *i.e.* the Pilbara, Canning and Kimberley (**Figure 1.1**; e.g. Semeniuk, 1993; IMCRA, 1998). All three of these regions are exposed to tropical cyclones, with, on average, five of these occurring along their coastlines annually (Lough, 1998; Australian Bureau of Meteorology, 2006).

The coastline of the most northern of the above regions, the Kimberley, is subjected to some of the largest tides in the world, *i.e.* with tidal heights in some areas exceeding 11m during spring tides (Eisma, 1997). Furthermore, as catchments in the Kimberley receive substantial rainfall (>1000 mm near Cape Londonderry, 13°43' S, 126°54' E), a number of major rivers discharge into the coastal waters of this region. The southernmost of the three regions, the Pilbara, experiences a more moderate tidal influence (3-6 m spring tides). The Pilbara has some rivers but their flow is strictly seasonal and usually restricted to periods of cyclonic activity.

The Pilbara and Kimberley regions are separated by the Canning region (**Figure 1.1**), whose coastline stretches from Cape Keraudren (19°57′ S, 119°46′ E) to Cape Leveuque (16°21′ S, 123°02′ E) and constituted the region in which the studies undertaken for this thesis were located. The climate of this region is arid, particularly towards the south, and consequently there are no major rivers along this coast (Semeniuk, 1996; Bird, 1997; Lough, 1998). Despite the lack of rivers, the nearshore, shallow waters of this region are very turbid due to large tidal water movements (8-10 m during spring tides).

A number of different types of nearshore habitats are present along the Canning coast due to the presence of such features as extensive areas of mangroves, rocky headlands, V-shaped bays and tidal lagoons (IMCRA, 1998). However, most of this coastline consists of extensive intertidal sand and mud flats. The largest of these is found at Eighty Mile Beach, a sandy calcareous dune system which stretches unbroken along *ca* 200km of the southern part of the region (Beard & Kenneally, 1993). These and other intertidal flats in the region contain a large and diverse invertebrate fauna (Pepping, 1999; Piersma *et al*., 1999, 2002), with the substantial benthic macro invertebrate component in turn supporting a high diversity and abundance of wading birds (Tulp *et al*., 1994; Tulp & de Goeij, 1994). The importance of the intertidal mud flats at Anna Plains (19°21′ S 121°19′ E) and southern Roebuck Bay (18°10′ S 121°19′ E) to migratory shorebirds has

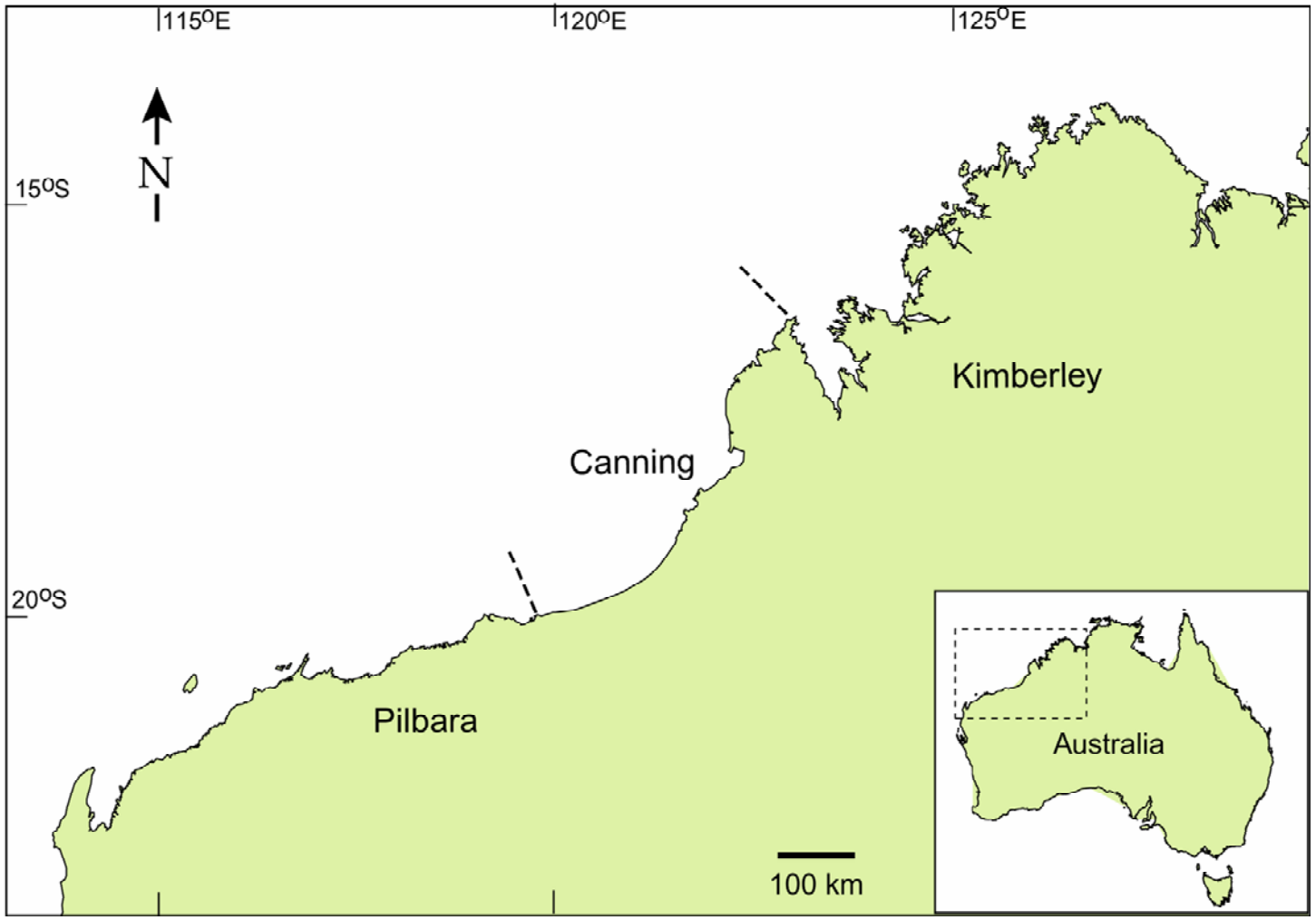

Figure 1.1. Map of north-western Australia showing the approximate boundaries between the Kimberley, Canning and Pilbara regions in north-western Australia.

led to their recognition as "Wetlands of International Importance" following the guidelines of the 1974 Ramsar convention on wetlands (Ramsar, 2004). The intertidal waters of the sand flats along the Canning coast also provide locations where the majority of the inshore commercial gill net fishery operates on this coast. This fishery predominantly targets the polynemids *Eleutheronema tetradactylum* and *Polydactylus macrochir* (see Chapter 1.3.3).

Due mainly to the extreme remoteness of north-western Australia, there has been relatively little research on the marine flora and fauna of the Kimberley, Canning and Pilbara regions. Most finfish research in these regions has concentrated on the mid to outer shelf and deep slope finfish resources, ***i.e.*** those in waters >30m deep, which are commercially exploited (***i.e.*** Newman, 2002a, b, c; Newman & Dunk, 2002, 2003). Similarly, studies of fish communities have concentrated mainly in deep water with soft substrates (Liu, 1976; Okera & Gunn, 1986; Sainsbury, 1987; Sainsbury *et al*., 1993; Williams *et al*., 2001). Although Travers *et al*. (2006) recently studied the fish communities in relatively shallow waters (*ca* 10-30 m) along all three bioregions, that study was restricted to a single habitat type, ***i.e.*** reef, and, as sampling was conducted with fish traps, it focused on relatively large fish.

The only major study of the use of nearshore habitats by fish was conducted in the Pilbara region near Dampier at 20°40' S, 116°40' E (Blaber *et al*., 1985; Blaber, 1986). The results of that study indicated that the juvenile fish in the nearshore, shallow waters of that region were subjected to heavy predation due to those waters being particularly clear, and thus facilitating the detection of prey by piscivorous fish. Since the juveniles of very few of the fish species found in water depths >20m on the North West Shelf were caught in nearshore waters, it was concluded that the latter waters did not constitute a significant nursery area for the commercially important deeper-water species of that region.

The list of fish species provided by Blaber *et al*. (1985) for the Dampier region is complemented by those compiled by staff at the Western Australian Museum for the Dampier Archipelago and the Kimberley region further to the north (Allen, 1992; Hutchins, 1995, 1996; 2001b, 2003, 2004; Morrison & Hutchins, 1997). Those studies further indicate that the composition of fish communities in nearshore waters are relatively distinct from those more offshore. Furthermore, while the nearshore fish fauna of the

Canning coast shares affinities with those of the Kimberley to the north and the Pilbara to the south, elements of these faunas are still distinct (Hutchins, 1999, 2001a; Fox & Beckley, 2005).

Despite the fact that finfish resources of the extensive nearshore areas of north-western Australia are being subjected to increasing pressure from commercial line fishers, shoreline gill net fishers and recreational anglers, there have been no studies of the fish assemblages in nearshore habitats along the Canning coast. Sound management plans for this important inshore resource require information on the species composition, and the distribution, abundance, habitat preferences and biology of the main species in the fish assemblages of this region.

1.3. The Polynemidae

1.3.1. Distribution, morphological characteristics and taxonomy

The Polynemidae (threadfins or tasselfishes) is a tropical percoid family that comprises approximately 40 species, which are found in coastal marine waters, estuaries and freshwater (Motomura, 2004a, b). The species in this family, some of which attain a relatively large size, typically live in shallow, turbid inshore waters, where they often occur in large numbers (Mukhopadhyay *et al.*, 1995; Motomura, 2004b). Some species of polynemid have a wide distribution. For example, *Polydactylus sextarius* and *P. plebius* are both found from the South African coast across India and Asia to Papua New Guinea and north to Japan (Motomura *et al*., 1999, 2001c), In contrast, other species, such as the freshwater *Polynemus kapuasenis*, *Polynemus melanochir dulcis* and *Polydactylus macrophthalmus*, may be restricted to single river drainages or lakes (Feltes 1999; Motomura *et al*., 2001h Motomura & Sabaj, 2002; Motomura & van Oijen, 2003).

The names threadfin and tasselfish refer to the characteristic possession by these fish of free lower pectoral rays. Furthermore, the etymology of *Eleutheronema* and *Polydactylus* refer respectively to the free-filament and many-fingered free rays of these genera. The detached pectoral rays, which vary in number from three to fifteen, depending on the species, are usually longer than the rest of the pectoral fin (**Plate 1.1**), and in some species extend further than the posterior margin of the anal or caudal fins.

Plate 1.1. A photograph of *Filimanus perplexa* caught in Indonesian waters. Note the enlarged free pectoral filaments that are characteristic of the Polynemidae (Photo: W. White).

The free pectoral filaments have a gustatory function, aiding the location of prey in turbid waters (Stead, 1906; Norman, 1975; Motomura *et al*., 2002e). There are also anecdotal reports that threadfin use their free pectoral filaments to herd small fish and prawns into balls, thereby facilitating their capture. Various dietary studies have shown that polynemids are typically benthic carnivores and important predators of small fish and crustaceans (Venkataraman, 1960; Onyia, 1973; Stanger, 1974; Riviera-Arriaga *et al.*, 1994; Salini *et al.*, 1990; Nasir, 2000). However, the dietary composition of a number of polynemid species varies with season, with prawns or juvenile fish making a greater contribution at different times of the year, and also undergoes size-related shifts, with the contribution of teleosts typically increasing with fish length (Malhotra, 1953; Rajan, 1968; Sumpton & Greenwood, 1990; Salini *et al.*, 1998).

The Polynemidae has typically been considered part of a percoid suprafamily, which also includes the Mugilidae (mullets) and the Sphyraenidae (barracudas) to which they are superficially similar (see Nelson, 1984). Indeed, on the basis of mitochondrial and ribosomal DNA studies Chen *et al.* (2003) concluded that the Polynemidae and the

Sphyraenidae were closely related, grouping together in a clade alongside the Carangidae, Echeneidae, Menidae, Centropomidae and Pleuronectiformes. Unfortunately, no members of the Sciaenidae were included in that study as it had recently been proposed, on the basis of studies of osteological characters and larval morphology, that the Sciaenidae and the Polynemidae are so closely related they should be united in a common superfamily, the Polynemoidea (Johnson, 1993; Leis & Trnski, 2004).

The Polynemidae has recently undergone considerable taxonomic revision (see for example Feltes, 1991, 1993; Motomura *et al*., 2001a-f, 2002; Motomura & Iwatsuki, 2001a,b; Motomura, 2002). This revision was required because of a lack of agreement regarding the classification of the genera within the family and the fact that synonyms are numerous. Furthermore, within Australia, taxonomic confusion has arisen as a result of the interchanging of common names of certain polynemid species and mistakes in popular literature and government publications (see for example Starling, 2005). A list of the polynemid genera and species currently recognised is given in **Table 1.1**.

1.3.2. Australian species of threadfin

Six polynemid species occur in Australian waters, of which the Blue Threadfin *Eleutheronema tetradactylum* (**Plate 1.2a**) and the King Threadfin *Polydactylus macrochir* (**Plate 1.2b**) grow to the largest size *i.e.* > 1000 mm TL. Both of these species contribute significantly to the commercial and recreational fisheries of Western Australia, Queensland and the Northern Territory. In addition, the Striped Threadfin *Polydactylus plebius,* which commonly reaches total lengths of *ca* 400 mm is targeted by recreational anglers and the smaller Australian Threadfin *P. multiradiatus* (250 mm max TL) makes a substantial contribution to the discarded by-catch of prawn trawl fisheries in Australian waters (Stobutzki *et al*., 2000; Motomura *et al*., 2002b). The two remaining species of polynemid found in Australian waters are the Blackfin Threadfin *Marginiserrula nigripinnis* and the Streamer Threadfin *Parapolynemus verekeri* (**Table 1.1**).

The Blue Threadfin *Eleutheronema tetradactylum*, also known as the Bluenose or Cooktown Salmon or the Fourfinger Threadfin, has a wide distribution ranging from the Persian Gulf in the west, China and southern Japan in the north and east to southern New

Table 1.1. List of the genera and species of the Polynemidae (Teleostei : Perciformes) (after Feltes, 1986; Motomura, 2004a,b). * denote species with a tropical Australian distribution.

Genus	Species	Authority	Genus	Species	Authority
Eleutheronema		(Bleeker)	***Polynemus* cont.**		
	tetradactylum *	(Shaw)		*melanochir melanochir*	Motomura and Sabaj
	tridactyulm	(Bleeker)		*multifilis*	Schlegal
	rhadinum	(Jordon & Evermann)		*paradiseus*	Linnaeus
Filimanus		(Myers)	***Polydactylus***		Lacepède
	heptadactylya	(Cuvier)		*approximans*	(Lay & Bennett)
	hexanema	(Cuvier)		*bifurcus*	(Motomura, Kimura & Iwatsuki)
	perplexa	Feltes		*longipes*	(Motomura, Okamoto & Iwatsuki)
	sealei	(Jordon & Evermann)		*macrochir* *	(Günther)
	xanthonema	(Valenciennes *in* Cuvier & Valenciennes)		*macrophthalmus*	(Bleeker)
	similis	Feltes		*malagasyensis*	(Motomura & Iwatsuki)
				microstomus	(Bleeker)
Galeoides		Günther		*mullani*	(Hora)
	decadactylus	(Bloch)		*multiradiatus* *	(Günther)
				octonemus	(Girard)
Leptomelonosoma		(Motomura & Iwatsuki)		*oligodon*	(Günther)
	indicum	(Shaw)		*opercularis*	(Gill)
				persicus	(Motomura & Iwatsuki)
Marginiserrula		(Feltes)		*plebius* *	(Broussonet)
	nigripinnis *	Munro		*quadrifilis*	(Cuvier)
Parapolynemus		Feltes		*romosus*	(Feltes)
	verekeri *	Saville-Kent		*sexfilis*	(Valenciennes *in* Cuvier & Valenciennes)
Polynemus		Linnaeus		*sextarius*	(Bloch & Schneider)
	aquilonaris	(Motomura)		*siamensis*	(Motomura, Iwatsuki & Yoshino)
	dubius	Bleeker		*virginicus*	(Linnaeus)
	hornadayi	Myers		*fossilis*	Daniltshenko
	melanochir dulcis	(Valenciennes *in* Cuvier & Valenciennes)			

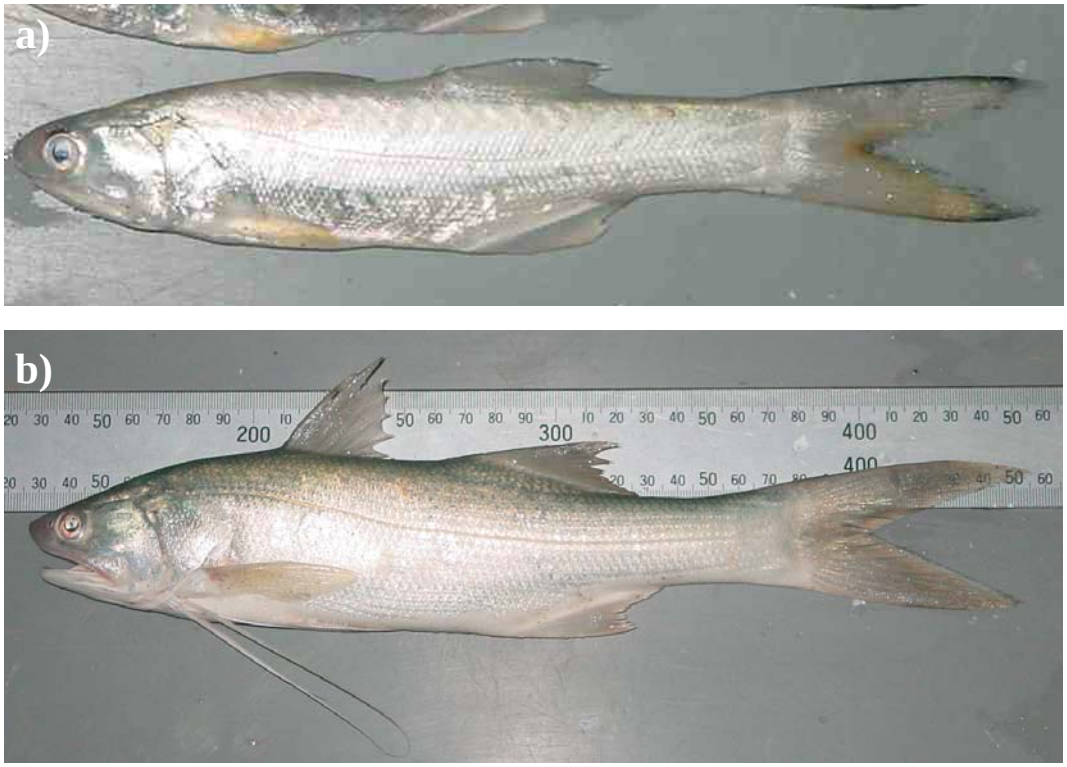

Plate 1.2. a) Blue Threadfin *Eleutheronema tetradactylum* (130 mm TL) and b) King Threadfin *Polydactylus macrochir* (331 mm TL) caught by seine netting at Eighty Mile Beach, Western Australia.

Guinea and Australia (Saleem *et al*., 1989; Janekitkarn *et al*., 1999; Motomura *et al*., 2001g). In Australian waters, *E. tetradactylum* has a tropical distribution, ranging from the Ashburton River in Western Australia to Sandy Cape in Queensland (**Figure 1.2**). Throughout its distribution, this species provides an important source of food for local populations and forms the basis of substantial commercial and artisanal fisheries (**Plate 1.3**) (Gopalakrishnan, 1972; Iwatsuki *et al*., 2000; Motomura *et al*., 2002a).

Polydactylus macrochir, commonly referred to as the Giant or King Threadfin or Burnett Salmon, is found only in northern Australia and southern Papua New Guinea (**Figure 1.3**). The single report of this species in India by Girija Kumari *et al*. (1985) is likely to be due to an erroneous identification (see Motomura *et al*., 2000). Within Australia, this species has been reported as extending from Broome in the west to the Brisbane River in the east (Motomura *et al*., 2000). However, the majority of the commercial fishery for this species in Western Australian waters occurs along the nearshore mud/sand flats in the region between Broome and Port Hedland. Furthermore, during the present study, *P. macrochir* was collected regularly from Karratha (20°40′S

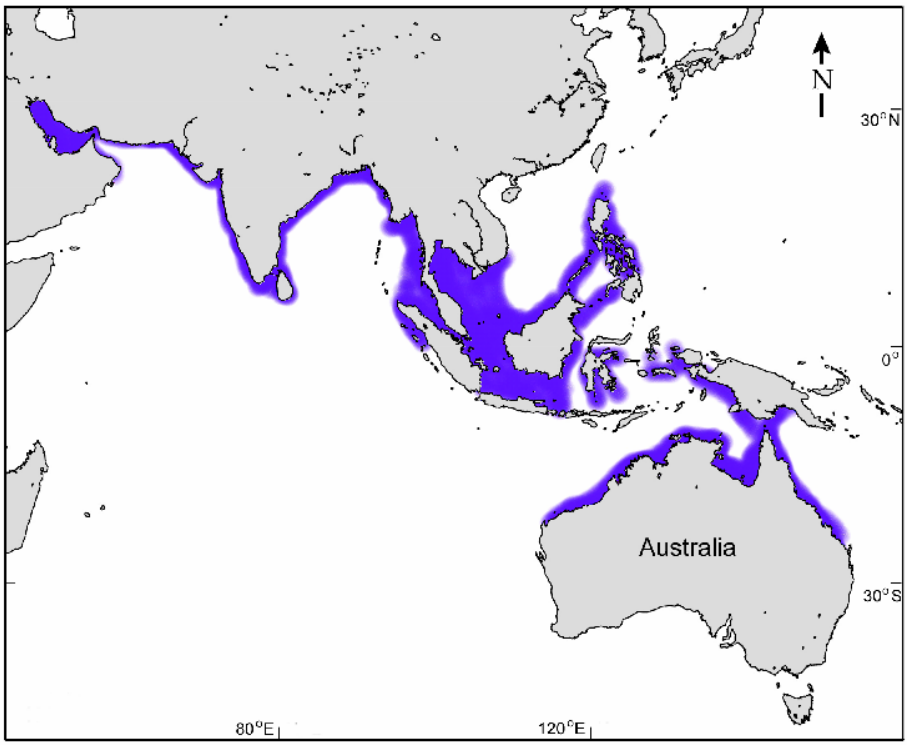

Figure 1.2. Distribution of Blue Threadfin *Eleutheronema tetradactylum*

Plate 1.3. Dried specimens of *Eleutheronema tetradactylum* offered for sale at street-side market in Java, Indonesia (Photo: S. deLestang).

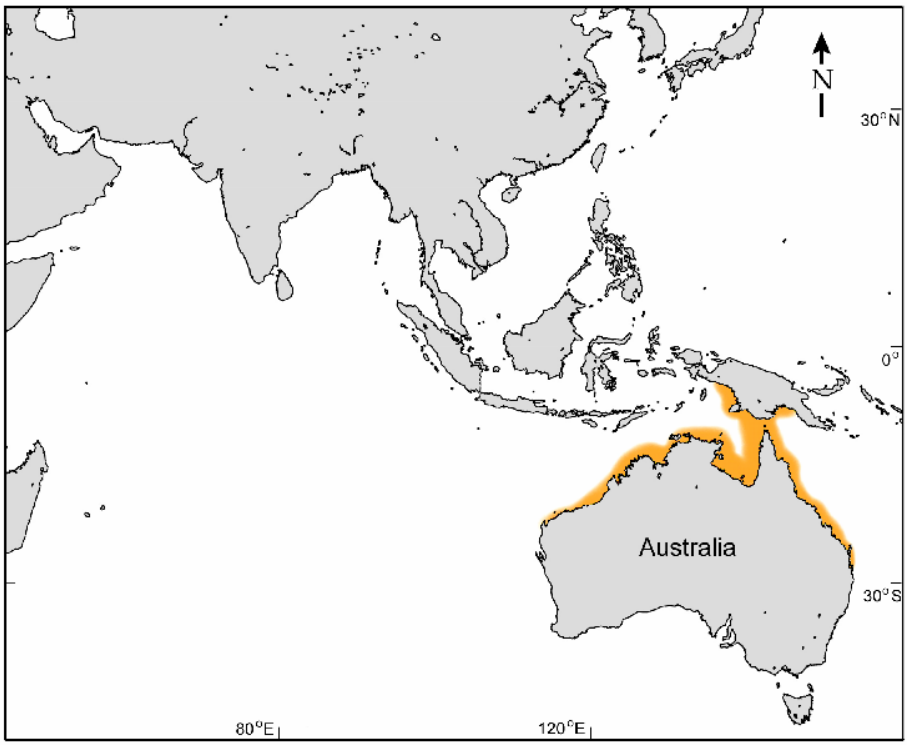

Figure 1.3. Distribution of King Threadfin *Polydactylus macrochir*

116°47′E) and reliable reports exist of large individuals of this species being taken at the southern end of Exmouth Gulf *ca* 500 km south and 900 km east of Broome (C. Skepper, pers. comm.).

1.3.3. Threadfin fisheries

Threadfin species are highly regarded for their eating qualities, forming the basis of important commercial, recreational and artisanal fisheries (Gopalakrishnan, 1972; Mukhopadhyay *et al.*, 1995; Iwatsuki *et al*., 2000; Motomura *et al*., 2002a) and are increasingly being used for aquaculture (*e.g.* Chao *et al*., 1994; Laidley & Liu, 2005; Ostrowski *et al*., 1996; Divakaran *et al*., 1999; Masuda & Ziemann, 2000, 2003). The world production of threadfin from wild sources and aquaculture collectively exceeded 0.5 million tonnes in each year between 1998 and 2000 (FAO, 2003). At a regional level, the fisheries for a number of threadfin species in certain parts of the world have undergone an alarming decline, which has been attributed, at least in part, to the failure of managers to appreciate the significance of fishing protandrous hermaphrodites (Abohweyere, 1989; Szyper *et al*., 1991; Bensam & Menon, 1994). In addition, the management of some

threadfin species is made more difficult as their juveniles are caught in large numbers as by-catch in prawn trawl fisheries (Isebor & Dare, 1995; Ambrose *et al*., 2005).

In Australia, the combined annual commercial catch of *E. tetradactylum* and *P. macrochir* in northern Australia averages between 800 and 1200 tonnes and is worth approximately $4 million annually (ABARE, 2005). The majority of the commercial threadfin catch in Western Australia is taken by the Kimberley Gill Net and Barramundi Managed Fishery (KGBMF), which operates northwards from Eighty Mile Beach to the Northern Territory boarder. The combined catches of *E. tetradactylum* and *P. macrochir* in the KGBMF have fluctuated between *ca* 70 and 110 tonnes in recent years, and typically contribute more than 60% to the total annual catch of this mixed species fishery (Department of Fisheries WA, Commercial Catch and Effort Statistics - CAES). The annual catch of threadfin in the KGBMF varies markedly and it has been suggested that this variation, particularly in CPUE, reflects fluctuations in the year to year abundance of these species (Newman & Harvey, 2005). In addition to the KGBMF catches, there is probably a further contribution of 60 to 80 tonnes by commercial fishers operating along the Pilbara coast (Newman & Harvey, 2005).

The Blue and King Threadfin species are important members of the inshore recreational fishery of the Pilbara and Kimberley coasts (Lyle *et al*., 2003), with a recent recreational fishing survey finding that the two threadfin species combined are the most popular species targeted by shore-based anglers in this region (Williamson *et al*., 2006). Recreational fishing pressure on these species will presumably continue to grow as the numbers of tourists visiting this coast each year increase and the populations of coastal centres in the Pilbara and Kimberley rise as a result of the forecast expansion in the resources industry over the following years (Anon, 2006b). Threadfins also have cultural significance for local aboriginal people and contribute an important source of food for their coastal communities (Davis, 1988; Pender, 1995; McArthur *et al*., 2000; Coleman *et al*., 2003). A small, but increasing, catch of threadfin is being taken by charter operators in both the Kimberley and Pilbara regions.

Although *E. tetradactylum* and *P. macrochir* are important to commercial, recreational and indigenous fishers in north-western Australia, they have not been the subject of any biological study in Western Australia. Research in north-eastern Australia,

and elsewhere in the case of *E. tetradactylum,* has shown that there is considerable variation in some aspects of the biology of these two species including the timing of spawning, the size and age at which they mature as males and change sex and, in the case of *E. tetradactylum*, whether they even undergo sex change (see Chapters 5.1; 6.1 for an overview of previous biological research on these two species). Regional variations in aspects of the biology and morphology of *E. tetradactylum* and other species of polynemid have been used in the past to distinguish between different stocks inhabiting Indian waters (Gupta, 1968, 1970, 1989). The possibility that, at least some of the variations among the biological characteristics exhibited by both *E. tetradactylum* and *P. macrochir* may be due to genetic differences among populations is consistent with the results of allozyme and mitochondrial DNA studies carried out by Keenan (1997) and Chenoweth & Hughes (2003), respectively. In view of this genetic subdivision, reliable information is required on the age compositions, growth rates, mortality and reproductive biology, including length and age at sex change, of the different Western Australian populations of threadfin to ensure that managers can develop appropriate plans for sustaining these resources.

1.4. Hermaphroditism in teleosts

The reproductive strategies exhibited by teleost fishes are the most diverse of all vertebrate groups (Bass & Groberb, 2001; Berra *et al*., 2004; Pietsch, 2005; Jalabert, 2005; Mank *et al*., 2006), of which the different types of hermaphroditism found across a diverse range of families are particular striking (Atz, 1964; Reinboth, 1970; Smith, 1975; Policansky, 1982). Hermaphroditism has been defined as the "existence of both the male and female sex in a single individual" (Atz, 1964). This definition is broad and Atz (1964) goes on to make a number of distinctions such as whether the hermaphroditism is normal, *i.e.* exists during some time of life across a large proportion of the population, and whether the hermaphroditism is functional, *i.e.* the individual functions as both male and female at sometime during its life. The definition given by Ross (1990) is useful as it excludes non-functional forms by stating that hermaphroditism in fish is "…the presence of both sex functions at some time during the life of an individual". Similarly, when determining whether a species is hermaphroditic, Sadovy & Shapiro (1987) stress the importance of

functionality of both sexes "…in a substantial proportion of individuals in a population...at some time during their life."

Functional hermaphroditism in teleosts may be classified as either synchronous (simultaneous) or sequential (Atz, 1964; Smith, 1975; Sadovy & Shapiro, 1987; Ross, 1990). Synchronous or simultaneous hermaphrodites are those in which individuals contain mature ovarian and testicular tissue at the same time and are thus effectively capable of functioning as both male and female simultaneously (Atz, 1964; Sadovy & Shapiro, 1987). Synchronous hermaphroditism has been reported in a number of fish families, but is most common in deep sea fishes of the Aulopiformes (Nelson, 1994) and among small coral reef-dwelling serranids such as the basslets (Reinboth, 1980; Warner, 1984). The small, mangrove inhabiting cyprinodontid *Rivulus marmoratus* is also a synchronous hermaphrodite and is believed to be the only vertebrate capable of self-fertilization (Harrington, 1971, 1974; Soto *et al*., 1992; Grageda *et al*., 2005).

Sequential hermaphroditism is the most common form of hermaphroditism and occurs when individuals function first as one sex and then, later, after undergoing a transition, as the other sex. When sequential sex change is from female to male, the hermaphroditism is termed protogyny. In contrast, the change from male to female is termed protandrous hermaphroditism. The sex change, whether protandrous or protogynous, is typically permanent and frequently involves a complete reorganisation of the gonad structure although the "terminal" gonad morphology may retain some ancestral characteristics (Sadovy & Shapiro, 1987). In contrast to the irreversible nature of most sequential sex change, some species, such as certain members of the Gobiidae, are able to change sex in either direction, depending on social cues, such as the loss of a mate (Sunobe & Nakazono, 1990, 1993; Nakashima *et al*., 1995; 1996; Kuwamura & Nakashima, 1998).

The evolutionary significance of sequential hermaphroditism has been the subject of hypotheses by a number of authors and most of these revolve around the size-advantage model (Ghiselin, 1969; Warner, 1975; Charnov, 1982; Muñoz & Warner, 2004). The size advantage model predicts that sequential hermaphroditism will evolve when there is a size-related difference in the reproductive success of either sex and that sex change will occur in the direction of that advantage (Ghiselin, 1969; Warner, 1988). Therefore, a

protogynous life history is favoured when the reproductive success of large fish is greatest for males. In contrast, protandry is selected for when the reproductive success of females becomes disproportionately greater than males with increasing size.

Protogyny is a common life history trait in tropical and sub-tropical reef fishes, with examples being widespread in the Serranidae, Lethrinidae, Labridae and Scaridae (Choat & Robertson, 1975; Robertson & Warner, 1978; Young & Martin, 1982; Shapiro & Rasotto, 1993; Bean *et al*., 2003). Such species typically exhibit a highly-organised social system, such as harems, with a tendency for one or a few males to be the largest individuals and for many smaller females to be present. In such a system, the reproductive success of small fish is expected to be greatest for females as the success of small males is likely to be minimal in the presence of a dominant male which may monopolise mating opportunities. Sex change in protogynous species is believed to be socially controlled and, in some species, has been experimentally initiated through the removal of the dominant males from the population (Robertson, 1972; Shapiro, 1981a, b, c; Benton & Berlinsky, 2006).

Protogynous hermaphrodites are either monandric or diandric, depending on how the males in the population are derived. In monandric species, all males in a population are secondary males, *i.e.* derived from functional females (see for example Shapiro, 1981c; Ferreira, 1993, 1995; Crabtree & Bullock, 1998; Brule *et al*., 2003; Fennessy, 2006). In contrast, the males of diandric species may be either secondary or primary males, the latter of which are derived directly from a juvenile form (Sadovy & Colin, 1995; Chan & Sadovy, 2002; Fennessy & Sadovy, 2002; Liu & Sadovy, 2004). The functionality of the female phase in secondary males is important as examples exist of species in which the males may develop from females that are yet to reach an advanced state of maturity and consequently have never functioned as females (Shapiro and Rasotto, 1993; Siau, 1994; Asoh, 2005). When all males in a population are derived directly from juveniles or females that never attained full maturity, the species is effectively gonochoristic (Asoh *et al*., 2001; Asoh, 2004).

A protandrous sex change is favoured over a protogynous life history when, with increasing size, the reproductive success of females becomes disproportionately greater than that of males. Such a situation typically exists when the reproductive success of

individual male fish is similar and largely independent of size, such as occurs in species that school or have difficulty in finding a mate or live in small, isolated populations (Ghiselin, 1969). In such a situation, sex change from male to female with increasing size maximises the reproductive success of an individual as the reproductive success of individual females is limited only by fecundity, which is typically a function of body size (*i.e.* Koops *et al*., 2004). Protandry has been observed in a large number of teleosts from a diverse range of habitats, including the open ocean, deep sea, coral reefs, estuaries and nearshore shallows (Reinboth, 1970; Warner, 1984; Ross, 1990). Furthermore, protandrous life histories have evolved repeatedly across a diverse range of teleost families, including the Clupeidae, Platycephalidae, Centropomidae, Creediidae, Muraenidae, Eleginopidae and Gonostomatidae (*i.e.* Aoyama *et al*., 1963; Okada, 1966; Fuji, 1970, 1971; Fisher, 1983; Badcock, 1986; Fishelson, 1990; Calvo *et al*., 1992; Blaber *et al*., 1996; Taylor *et al*., 2000; Shinomiya *et al*., 2003; Langston, 2004).

The most intensively studied and understood examples of protandry are found in the anemonefishes of the Pomacentridae (*i.e.* Fricke & Fricke, 1977; Ochi, 1989: Kuwamura & Nakashima, 1998; Miura *et al*., 2003). Sex change in anemonefish is socially controlled and, in most of these species, the mating system is typically monogamous, with a larger and dominant female pairing with a smaller male (Yanagisawa & Ochi, 1986; Buston, 2003; Hattori, 2005). These pairs frequently share their anemone with a number of juveniles or immature males forming a colony and the loss of the female typically initiates the protandrous inversion of the largest male to a female and the subsequent replacement of the male through maturation of a subordinate. However, the males of some species of anenomefish favour an inter-host migration in search of a female rather than initiate the costly process of sex change following mate loss (Ochi, 1989; Hattori, 2005). Futhermore, while the females of most species develop from males, the females of at least one species, *Amphiprion clarkii*, may develop from immature males, as well as mature males (Hattori & Yanagisawa, 1991). *Amphiprion clarkii* is therefore effectively digynic, *i.e.* an example of a protandrous hermaphrodite that has two pathways for the development of females (see Sadovy & Shapiro, 1987). Digyny is a rare condition among protandrous fishes, with only a few other examples having been recorded, these

occuring in the Latidae, Clupeidae, Sparidae and Polynemidae (Longhurst, 1965; Moore, 1979; Pajuelo & Lorenza, 2004; Blaber *et al*., 2005).

Although the socially-controlled version of protandry observed in the Pomacentridae has received considerable attention, it is not the typical mating system of protandrous fishes. The Sparidae, a family recognised for the plasticity of its sexual expression, contains a large number of protandrous species (Yeung & Chan, 1987; Buxton & Garratt, 1990). The majority of protandrous sparids form schools or mixed-size spawning aggregations in which all male fish have similar reproductive success and spawning events are not monopolised by individuals, as in haremic societies (Warner, 1988). The gonads of sparids are represented by ovotestes, in which each gonadal lobe consists of a medio-dorsal ovarian zone that is separated from a latero-ventral testicular zone by a wall of connective tissue. Although individuals typically possess both tissue types throughout their life, only one type is functional during different stages (Besseau & Bruslé-Sicard, 1995; Lone *et al*., 2001; Hesp *et al*., 2004). In protandrous species, the ratio of individuals functioning as females increases with increasing length and age (Micale & Perdichizzi, 1994; Bruslé-Sicard & Fourcault, 1997; Tobin *et al*., 1997; Lone *et al*., 2001).

Another family in which the process of protandrous sex change has received considerable attention is the Latidae, to which the Barramundi *Lates calcarifer* is now allocated (see Otero, 2004). Sex change in Barramundi, which appears strongly related to growth rate, involves a total reorganisation of the gonads and typically occurs rapidly shortly after the spawning season (Moore, 1979; Davis, 1982, 1986; Guiguen *et al*., 1994). An understanding of the reproductive biology of Barramundi is further complicated by the fact that, within a population, some individuals may undergo precocious maturity and sex change, whereas others are either primary or secondary females (digynic) and yet others either never change sex or spawn (Moore, 1979; Davis, 1984 Milton *et al*., 2005).

The Polynemidae, like the Sparidae and Latidae, displays a variety of reproductive life history strategies. Although the majority of threadfin species are apparently protandrous hermaphrodites, a few are gonochoristic (*cf*; Hida, 1967; Kagwade, 1970; Dorairaj, 1973; Santerre & May, 1977; Dentzau & Chittenden, 1990). Furthermore, one of the protandric species of threadfin is digynic, with females derived either from an immature form or from functional males through sex change (Longhurst, 1965). There is

also evidence that some threadfin may be hermaphroditic in certain regions and gonochoristic in others. For example, *Eleutheronema tetradactylum* is reported to be protandrous in eastern Australia (Stanger, 1974; Russell, 1988; McPherson, 1997), but gonochoristic in India (Patnaik, 1967, 1970; Gopalakrishnan, 1972) and Singapore (Chao *et al*., 1994).

1.5. Management of hermaphroditic fishes

The sustainable management of a species with a life history that departs from gonochorism, such as that exhibited by sequential hermaphrodites, poses a further challenge for fisheries managers and depends on a thorough appreciation of the life history of the species in question. For example, fishing-related mortality is rarely independent of size and age as the largest individuals are typically targeted by fishers. In such a scenario, the mortality experienced by each sex may be very uneven if the larger individuals in a population are biased toward a particular sex, as is typically the case in sequential hermaphrodites.

In protogynous species, such as many serranids and labrids, in which the direction of sex change is from female to male, the largest and oldest individuals experiencing the greatest fishing mortality are typically males (Russ, 1991; Levin & Grimes, 2002). This can have varied and drastic consequences. For example, heavy exploitation may lead to a reduction in the abundance and mean length of males compared with unexploited populations (Thompson & Munro, 1978). Furthermore, the reproductive success of a population may be reduced due to the loss of the largest and presumably most fecund females through fishing mortality and sex change as it is typically the largest females in haremic populations that initiate sex change when males are removed (Vincent & Sadovy, 1998; Adams *et al*., 2000). In extreme situations, high mortality of males during or immediately prior to spawning may lead to sperm limitation, which has a further impact on the spawning success of the population and may severely restrict the number of larval recruits (Bannerot *et al*., 1987; Coleman *et al*., 1996; Alonzo & Mangel, 2004). This reduction in the strength of recruitment through a decrease in the effective spawning biomass is referred to as recruitment overfishing and may ultimately result in the crash of

the fishery and which is then difficult to reverse (Russ, 1991; Bohnsack, 1993; Hutchings, 2000; Frank & Brickman, 2001). In addition to the consequences of sexually-biased fishing mortality outlined above, many protogynous hermaphrodites are also particularly susceptible to fishing pressure as they typically experience low natural mortality, take many years to reach maturity and are territorial or form spawning aggregations (Sadovy, 1996; Musick, 1999; Huntsman *et al*., 1999; Whiteman *et al*., 2005; Fennessy, 2006).

Protandrous species, *i.e.* those that change sex from male to female, are equally at risk from high exploitation. Sperm limitation, as seen in protogynous species, is unlikely to occur with the majority of protandrous species, which are typically group spawners with many males and fewer, larger females. However, protandrous species are particularly susceptible to recruitment overfishing as it is typically the large, highly fecund females that are lost through fishing mortality, which has considerable consequences for the number of eggs and larvae that are available for future recruitment (Milton *et al*., 1998; Ziemann & Cantrell, 1998; Friedlander & Ziemann, 2003). Examples of the effects of heavy fishing effort biased toward females can be seen in the protandrous clupeids *Tenualosa macrura* and *T. toli* in Sumatra and Sarawak, which suffered alarming declines in catches during the early 1990s (Blaber *et al*., 2005). These declines prompted an investigation into the life histories of these two clupeids and this revealed that both species were protandrous, the first recorded case of such hermaphroditism in the Clupeiformes (Blaber *et al*., 1996). The traditional fisheries for these short-lived species had largely targeted fish in their second year of life, which, while presumably having previously spawned as males, were yet to spawn as females (Blaber *et al*., 1999).

The importance of recognising and understanding the consequences of a protandrous life history is further highlighted by the decline that has occurred in the fisheries for a number of protandrous polynemids from around the world, *i.e.* Abohweyere (1989), Szyper *et al*.(1991), Bensam & Menon, (1994), Kizhakudan & Kizhakudan (2005). One of the best-studied examples of a heavily-fished polynemid is that of the Moi *Polydactylus sexfilis* in Hawaii. The catches of this sought-after threadfin, once reserved for the royal table, declined drastically by *ca* 90% over the last four decades (Szyper *et al*., 1991). This decline was due mainly to the break down of recruitment resulting from continued overfishing of the larger female fish (Kelley *et al*., 1995; Friedlander &

Ziemann, 2003; Poepoe *et al*., 2003). In addition to the bag limits already in place, stock enhancement has been successfully employed as a tool for the management of *P. sexfilis* in Hawaii (Leber *et al*., 1995; Friedlander & Ziemann, 2003). Cultured juveniles released into nursery areas have bolstered the recruitment of wild juveniles and have been shown to add to the stock of mature females (Friedlander & Ziemann, 2003). Similarly, aquaculture production of *P. sexfilis* has recently received significant interest as a means of alleviating fishing pressure on wild stocks (Szyper *et al*., 1991; Chambers *et al*., 2001; Kam *et al*, 2002, 2003).

Another strategy available to fisheries managers attempting to ensure the sustainability of sequential hermaphrodites (both protandrous and protogynous species) is the introduction of a maximum size for retention, which ensures that the largest individuals in the population, either males or highly fecund females, are spared from harvest (Conover & Munch, 2002). Such an approach is commonly implemented for large, protogynous groupers (Serranidae) (see for example 1000 mm TL maximum size for selected groupers in Western Australian waters. Anon, 2005). A maximum length for retention is also one of the options implemented in the management of the protandrous Barramundi *Lates calcarifer* in Western Australia. This ensures that fish greater than 800 mm, which are typically highly fecund females that are likely to have significant reproductive success, are returned live to the water (Anon, 2005). Equally, the protection of these larger individuals may be achieved through a change in fishing practices that alters the size range of targeted fish, such as reducing the size of gill net mesh permitted in a fishery, as has been suggested in the management of *L. calcarifer* (Milton *et al*., 1998).

An alternate direction is the creation of no take zones or marine protected areas (MPAs) where all individuals are protected from fishing for all or at least part of the year (eg. Beets & Friedlander, 1999; Jamieson & Levings, 2001; McClanahan & Graham, 2005; Valentine & Heck, 2005). This approach can be particularly valuable in protecting territorial species with high site fidelity and those species that form spawning aggregations, such as protogynous serranids and labrids (Coleman *et al*., 1999; Adams *et al*., 2000; Russ, 2002; Sadovy & Domeier, 2005). The use of MPAs has also been shown to be a useful tool for managing protandrous species in Australia. In a study of river systems open and closed to fishing in Queensland, Ley & Halliday (2003) recorded a 4.5

times greater mean biomass of Barramundi per large-mesh gillnet set in closed systems than in estuaries open to commercial fishing. Not only were the numbers and size of mature Barramundi greater in rivers closed to fishing but so also were the numbers of juvenile Barramundi recorded, possibly indicating that juvenile recruitment of this protandrous species, within rivers open to fishing, had been adversely affected by high fishing pressure (Halliday *et al*., 2001; Ley *et al*., 2002). This finding is not surprising as Ley & Halliday (2004) revealed that estimates of total egg production for Barramundi in rivers closed to fishing were up to 21 times higher than those for rivers open to fishing. Ley & Halliday (2004) concluded that a system of MPAs may actually be essential in maintaining a sustainable fishery for the protandrous Barramundi in northern Australia.

1.6. Main objectives of the study

The overall aim of the first section of the thesis was to obtain, for the first time, sound quantitative data on the fish faunas of nearshore, shallow waters along the Canning coast of north-western Australia. Thus, the fish fauna in nearshore waters was sampled at three widely- spaced locations, Port Smith, Eighty Mile Beach and Cape Keraudren, along this coast, with the view to determining the following. 1) The extents to which the diversity, abundance and species composition of the fish faunas of the Canning coast are influenced by location, habitat and time of year. 2) Which species use bare sand, mangroves and/or intertidal pools as nursery areas and which are permanent residents in one or more of those habitats. 3) Identification of the commercial and recreational fish species found in each of the above three habitat types and their relative abundance in those habitats.

The overall aim of the second section of the study was to obtain reliable data on the reproductive biology, age compositions, growth rates and mortality of *E. tetradactylum* and *P. macrochir* in Western Australia. The individual aims, which were the same for both species, were as follows. 1. Confirm that, as elsewhere in Australia, these species are protandrous hermaphrodites in Western Australia. 2. Determine the length and age at which sex change from male to female occurs. 3. Determine the length and age at which maturity is attained by males. 4. Determine the timing and duration of the spawning period and whether fecundity is determinate or indeterminate and if

spawning occurs on several occasions during a spawning period. 5. Establish a reliable estimate of the length/weight relationship for use in stock assessment models. 6. Validate that opaque zones are laid down in otoliths annually and that these growth zones can be used to reliably age fish. 7. Determine the size and age compositions and growth characteristics. 8. Estimate total, natural and fishing mortality. 9. Estimate the current level of yield per recruit, spawning biomass per recruit and spawning potential ratio.

2. General Materials and Methods

2.1. Sampling of fish communities of the north-western Australian coast

2.1.1. Locations and habitats sampled

The fish in nearshore, shallow waters at Port Smith, Eighty Mile Beach and Cape Keraudren on the Canning coast of north-western Australia (**Figure 2.1**) were sampled using seine and gill nets and the ichthyocide rotenone. This range of sampling methods enabled a number of different habitats to be sampled, including bare sand shorelines, mangroves and intertidal pools. The samples collected from the above three locations by different methods were used to determine how the characteristics of the fish communities varied with habitat type, location and time of year. Although the seine net and gill net samples also provided the main source of individuals for the studies of the Blue Threadfin *Eleutheronema tetradactylum* and the King Threadfin *Polydactylus macrochir*, they were supplemented by samples collected from other regions by the same methods and from commercial and recreational fishers (see Chapter 5.2). Note that no threadfin were caught in the intertidal pools.

The northernmost of the three sampling locations, *i.e.* Port Smith, 18°30′ S, 121°47′ E, is *ca* 100 km south of Broome and *ca* 2250 km north of Perth (**Figure 2.1**). This sampling location consists of a large tidal lagoon formed by a breached dune ridge and is an example of the dominant type of bay found in this area (**Figure 2.1a**). The lagoon, which runs along the landward side of the dune ridge, is fringed by an extensive (*ca* 670 ha) mangal development that is dominated by *Rhizophora stylosa* and *Avicennia marina*. On high spring tides, the fringing mangroves are inundated, but, as the tide recedes, the lagoon almost totally empties through a deep entrance channel connecting the lagoon to the ocean (**Plate 2.1**). On low spring tides, vast areas of sand and broken shell become exposed, with water remaining only near the entrance channel of the lagoon and in intertidal pools which vary in size. The large tidal movement, in combination with the narrow entrance channel, results in most areas of the lagoon experiencing high current velocities during spring tides.

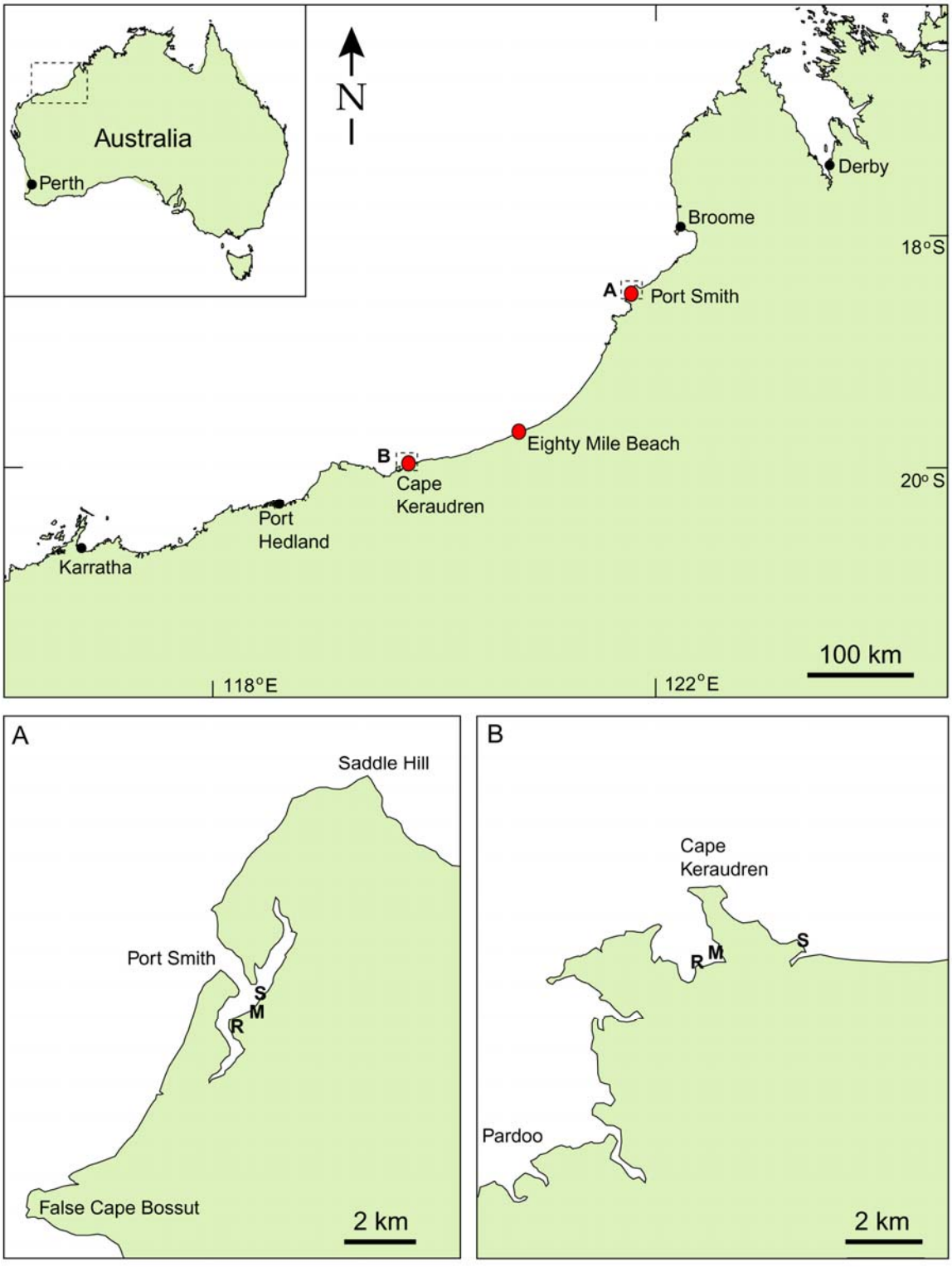

Figure 2.1. Map of the Canning coast of north-western Australia showing the coastal locations where the nearshore, shallow water fish communities were sampled, *i.e.* Port Smith, Eighty Mile Beach and Cape Keraudren (top). In A and B (and subsequent plates), the letters M and S refer to mangrove and bare sand sampling sites and R to the location of intertidal pools where rotenone was used.

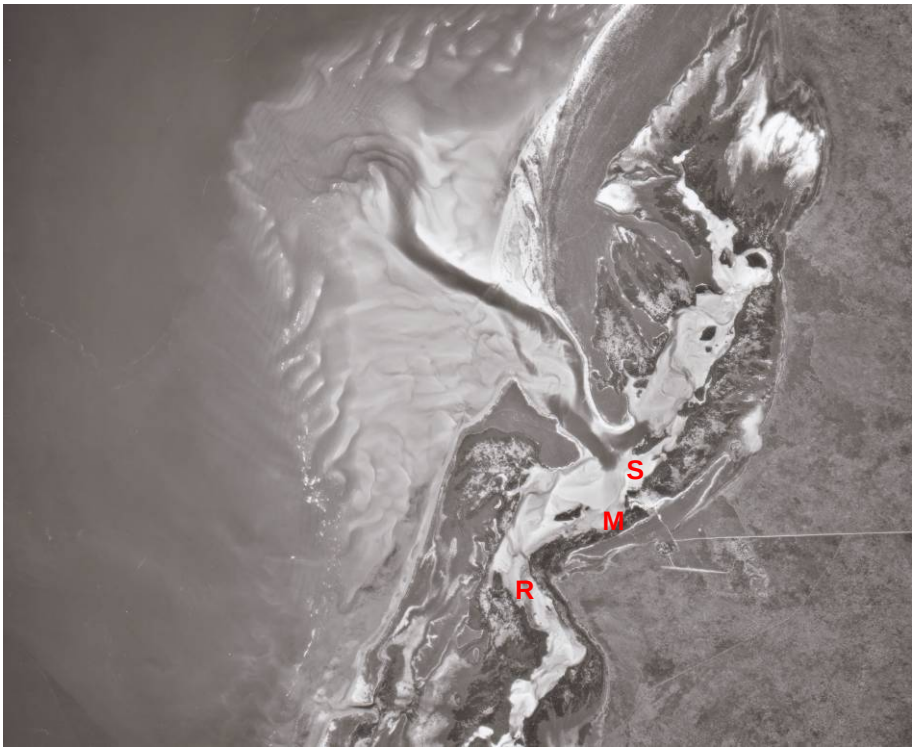

Plate 2.1. Aerial photograph of the lagoon at Port Smith showing the fringing mangrove habitat and the sand banks exposed at low tide.

The central sampling location, *i.e.* near the middle of the 220 km long Eighty Mile Beach, was located close to Wallal Station at 19°45′ S, 120°40′ E, approximately 175 km to the south west of Port Smith (**Figure 2.1**). It has a north-west orientation, a very slight gradient and no creeks or rocky outcrops in its vicinity (**Plate 2.2**). The slight gradient of the beach sampled at Eighty Mile Beach, in combination with the large tidal range (>8m), results in very large areas of sand, silt and mud becoming exposed during low spring tides, with the distance between the high and low water marks often exceeding 2000 m.

The southernmost sampling location, *i.e.* Cape Keraudren at 19°57′ S, 119°46′ E, is situated *ca* 150 km north east of Port Hedland and *ca* 300 km south west of Port Smith (**Figure 2.1**). The rocky headland at Cape Keraudren marks the southern boundary of Eighty Mile Beach (**Figure 2.1b**). An area of *ca* 760 ha of relatively extensive mixed mangal environment with moderate tidal creek development is located immediately to the south west of Cape Keraudren (**Plate 2.3**). Although *Rhizophora stylosa* and *Avicennia marina* are the dominant species of mangrove in this area, other mangrove species, such as *Osbornia octodonata*, *Bruguiera exaristata*, *Aegiceras corniculatum*, *Ceriops tagal*,

Plate 2.2. Aerial photograph of the region sampled at Wallal Station on Eighty Mile Beach.

Plate 2.3. Satellite image of Cape Keraudren showing extensive intertidal flats, moderate mangrove development and the southern limit of Eighty Mile Beach stretching to the north east (DOLA).

Excoecaria agallocha, and *Aegialitis annulata,* are present (Paling, 1996). On low tides, the water recedes from the mangroves leaving small to medium-sized tidal pools and exposing extensive intertidal platforms of silt and rock. Similar examples of this type of headland and bay complex exist to the south west.

2.1.2. Sampling regimes

The fish faunas at Cape Keraudren, Eighty Mile Beach and Port Smith were each sampled four times in both 12 month periods between December 2000 and November 2002. Thus, each of the locations was sampled twice in each of the following "seasons": early wet (November to January), late wet (February to April), early dry (May to July) and late dry (August to October) (**Table 2.1**).

The fish faunas over bare sand at Port Smith, Eighty Mile Beach and Cape Keraudren were sampled using a 60.5 m long seine net (Chapter 3.2). Three replicate seine net samples were obtained during the day from two sites over bare sand at Port Smith, the southernmost of which was located close to mangroves (**Figure 2.1a**), and from two sites (subsequently referred to as the northern and southern sites) at Eighty Mile Beach that were separated by approximately 2.5 km. Three replicate seine net samples were also collected during the day from a site just to the east of Cape Keraudren (**Figure 2.1b**). The extensive mangrove and rock habitats and limited sandy areas at Cape Keraudren consequently meant that only a single site could be sampled with the seine net at this location.

The 60.5 m seine net consisted of two 29 m long wings, each made of 25 mm mesh, and a 2.5 m bunt consisting of 9 mm mesh. This net fished to a depth of 2.5 m and swept an area of 583 m^2. The seine net was either laid in a semi-circle from the bow of a boat until fully extended or walked out from the beach and extended parallel to the shore and then dragged rapidly towards and then on to the shore (**Plate 2.4**). Each site was sampled during the neap tidal phase, when the height of the tide was at or close to its maximum and water movement was least. Sampling was not undertaken at night because of the potential for shark and crocodile attacks.

Table 2.1. Sampling regimes at Port Smith, Eighty Mile Beach and Cape Keraudren. Samples were collected on each occasion (*) using a 60.5 m long seine net, rotenone and a 60 m long composite monofilament gill net, except during extreme cyclonic weather conditions (c). Mean monthly values for rainfall and mean maximum air temperature in the study region are shown. ns = no sample

Method	Region	Habitat	Early Wet			Late Wet			Early Dry			Late Dry		
			Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Seine Net	Port Smith	a) bare sand	*	*		*	*		*	*		*		*
		b) near mangroves	*	*		*	*		*	*		*		*
	80 Mile Beach	a) bare sand (north)	*	*		c	*		*	*		*		*
		b) bare sand (south)	*	*		*	*		*	*		*		*
	Cape Keraudren	a) bare sand	*	c		c	*		*	*		*		*
Rotenone	Port Smith	intertidal pools	*	ns		*	ns		*	*		*		*
	Cape Keraudren	intertidal pools	*	ns		*	ns		*	*		*		*
Gill net	Port Smith	a) bare sand	*	*		*	*		*	*		*		*
		b) mangroves	*	*		*	*		*	*		*		*
	80 Mile Beach	a) bare sand	*	*		*	*		*	*		*		*
	Cape Keraudren	a) bare sand	*	c		c	*		*	*		*		*
		b) mangroves	*	c		c	*		*	*		*		*

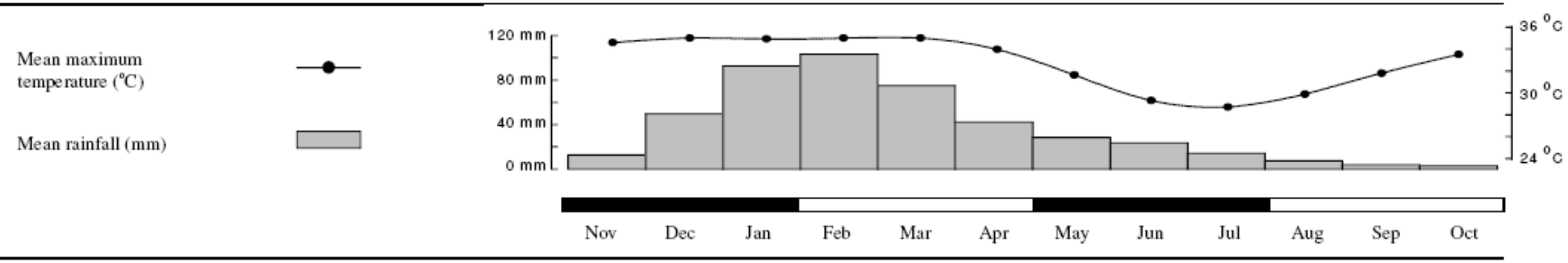

Plate 2.4. The 60.5 m seine net being deployed over bare sand close to mangroves at Port Smith.

The ichthyocide rotenone was used on six occasions to collect fish from three randomly-selected intertidal pools at both Port Smith and Cape Keraudren (Chapter 3.2). Powdered rotenone was first mixed with water to form a paste before being added to the pool in a concentration of *ca* 200 g of dry rotenone powder 10 m^{-2} of pool area. Every effort was made to ensure that neighbouring pools did not become contaminated with rotenone, which included constructing barriers to stop water moving out of the treated pool until it was diluted by the incoming tide. The pools sampled ranged from 10 to 20 m^2 in area and were up to 0.4 to 0.6 m in depth (**Plates 2.5, 2.6**). Ten minutes after rotenone treatment, the fish in the pools were sampled with a long-handled scoop net constructed of 5.0 mm mesh. Each pool was monitored and resampled for 1 h after the initial dose to allow for the differential susceptibility of certain fish taxa.

The bare sand habitats at Port Smith, Eighty Mile Beach and Cape Keraudren, and the mangroves at the first and last of these locations, were sampled using a 60 m composite gill net (see Chapter 4.2). This gill net was 2 m high and consisted of six 10 m long monofilament panels, each with a different stretched mesh width of either 51, 76, 102, 127, 152 or 178 mm. The gill net was set parallel to the shoreline at low to mid tide and, using fencing pickets, was fixed in a position which would ensure that it would be

Plate 2.5. An intertidal pool at Port Smith, which was sampled with rotenone, showing sandy sediment and rock/oyster habitat.

Plate 2.6. An intertidal pool at Cape Keraudren, which was sampled with rotenone, showing overhanging mangroves and fringing mangrove pneumatophore habitat.

covered by the incoming tide to a maximum depth of approximately 1.5-2.0 m for *ca* 3h (**Plates 2.7, 2.8**). When sampling mangroves, the gill net was extended parallel to the shoreline and attached to mangrove trunks in an area where it would likewise be covered to a maximum depth of 1.5-2.0 m for 3h at high tide (**Plate 2.9**). Gill netting was always conducted on spring tides and during darkness. On each sampling occasion, the gill nets were set four times in each habitat and on different nights.

2.1.3. Fish collection and processing

The fish in each replicate sample obtained from each location were placed in an ice slurry and transported to a mobile laboratory. They were identified to species and measured to the nearest 1 mm (total length), except when the number of fish was large, in which case the lengths of fish in a randomly-selected subsample of 100 fish were measured. The individuals of each species in each replicate sample were counted and the total wet weight of all individuals of each species in each replicate sample was weighed to the nearest 0.1 g. The number and biomass of fish in each replicate seine net catch were converted to a density, *i.e.* number of individuals 500 m^{-2} and weight (kg) 500 m^{-2}, respectively. Similarly, the number and biomass of fish in each replicate rotenone sample were converted to number of individuals 10 m^{-2} and weight (g) 10 m^{-2}, respectively. The numbers and biomass of each species caught in each set of a composite gill net were converted to a catch rate, *i.e.* number of fish $3h^{-1}$ and the weight (kg) $3h^{-1}$, respectively.

2.2. Environmental parameters

Salinity and water temperature were recorded at each site after each sampling occasion. Records were also kept of the time of sampling, the state of the tide, lunar period and weather conditions. When sampling intertidal pools with rotenone, records were also kept of pool area, maximum and average water depth and the percentage cover of any sand, oysters, algae, mangrove pneumatophores, submerged snags and mangrove canopy cover.

Plate 2.7. The composite gill net staked out on the foreshore at Eighty Mile Beach prior to inundation at low tide.

Plate 2.8. The composite gill net staked out on the foreshore at Eighty Mile Beach at high tide. Note that all gill netting to sample the fish fauna in unvegetated habitats and mangroves (Chapter 4) was conducted during darkness. Gill nets were only used opportunistically during daylight hours to sample for threadfin (Chapters 5, 6)

Plate 2.9. The composite gill net set in mangrove habitat at low tide prior to being inundated.

3. Fish faunas of nearshore, shallow waters and intertidal pools

3.1. Introduction

The shallow waters of temperate and tropical estuaries provide highly productive and protected habitats, which act as important nursery areas for the juveniles of certain species of marine teleost (Haedrich, 1983; Claridge *et al*., 1986; Whitfield, 1999; Potter & Hyndes, 1999; Blaber, 2000). A similar nursery function is performed for several fish species by the shallow waters of sheltered parts of the coastline, such as those found in embayments (e.g. Lasiak, 1981; Brown & McLachlan, 1990; Blaber *et al.*, 1995; Santos & Nash, 1995; Hyndes *et al*., 1996b; Dahlgren *et al*., 2006). The nursery role played for fishes by the latter nearshore coastal waters will be particularly important for such species in those arid zones where rivers, and thus estuaries, are scarce or absent (e.g. Lenanton & Potter, 1987), as is the situation in the Canning region of north-western Australia.

The compositions of fish faunas in habitats in nearshore coastal and estuarine waters, such as those of unvegetated sand, seagrass and mangroves, often differ markedly (*e.g.* Jenkins & Wheatley, 1998; Guidetti, 2000; Nagelkerken & van der Velde, 2004; Nero & Sullivan Sealey, 2005). Such differences in the community structure of fish assemblages in different habitats reflect differences in the habitat preferences of species (*i.e.* Jenkins & Hamer, 2001; Gibson *et al*., 2002; Upston & Booth, 2003). Thus, for example, species such as *Pseudorhombus jenynsii*, *Engyprosopon grandisquama* and *Lesueurina platycephala* have a strong preference for unvegetated areas (Travers & Potter, 2002; Valesini *et al*., 2004), whereas pipefishes of the genus *Stigmatopora* and a number of odacid species are most abundant in seagrass (Jenkins & Wheatley, 1998; MacArthur & Hyndes, 2001) and the juveniles of *Acanthopagrus latus* are found predominantly in mangroves (Blaber *et al*., 1985; Hesp, 2003).

Intertidal pools have been shown to constitute valuable nursery habitats for certain teleosts in temperate Australia (Lardner *et al*., 1993; Griffiths, 2003a, b; Griffiths *et al*., 2003) and other parts of the world (Kneib, 1987; Beckley, 1985a, b, 2000; Barreiros *et al*., 2004; Castellanos-Galindo *et al*., 2005). The only study of the fish faunas of intertidal pools in Western Australia is that of Blaber *et al.* (1985), which was conducted at Dampier

in the Pilbara region of the north-western part of the state. Virtually nothing is known about the species using this type of habitat elsewhere in tropical Australia. Furthermore, none of those studies that have investigated the fish fauna of intertidal pools in other parts of the world have directly compared the fish fauna inhabiting those intertidal pools with that of the surrounding shallow, nearshore unvegetated waters.

The use of non-metric multidimensional scaling ordination has been particularly effective in demonstrating that the species compositions of the ichthyofauna of certain estuaries undergo very well-defined cyclical changes during the year (Potter *et al.,* 1997; Thiel & Potter, 2001; Hoeksema & Potter, 2006). These changes were shown to be attributable to time-staggered patterns of immigration and emigration of certain species, and particularly in the case of the first two studies, which were conducted in northern hemisphere macrotidal estuaries, of the juveniles of marine species. Similar annual cyclical changes in species composition in the fish fauna inhabiting nearshore unvegetated and inshore seagrass habitats in marine waters have been shown to occur in a large sub-tropical embayment in Western Australia (Pember, 1999; Travers & Potter, 2002). There has been, however, no attempt to use appropriate statistical methods to determine whether the fish communities of shallow, nearshore waters along any region of north-western Australia undergo annual cyclical changes and, if so, which species are driving those changes.

The overall aim of this section of the thesis on the Canning coast of north-western Australia was to obtain sound quantitative data on the characteristics of the ichthyofauna of nearshore (along shoreline), shallow waters and intertidal pools, respectively, of this region. For this purpose, nearshore waters were sampled with a seine net with a fine mesh (9mm), while intertidal rock pools were sampled using rotenone, and thus, in both cases, would facilitate the capture of small fish. The sampling of shallow, nearshore waters in three regions, *i.e.* Port Smith, Eighty Mile Beach and Cape Keraudren, and of the intertidal pools present in only the first and third of those region, allowed the following hypotheses to be tested. 1) The ichthyofaunas of those two habitat types will be dominated by the juveniles of some large and medium-sized species, which use inshore waters as a nursery area, and by small species, such as those belonging to the Atherinidae, which typically spend the whole of their life cycle in nearshore waters. 2) The number of species and

density of fish in these communities will change during the year, as a result of differences in the timing and strength of recruitment of the different species. 3) Consequently the compositions of the ichthyofauna will undergo regular and consistent intra-annual cyclical changes. 4) The composition of the ichthyofauna inhabiting intertidal pools will be distinct from that inhabiting shallow, nearshore waters, distinguished predominantly by species belonging to families which are frequently residents of intertidal pools such as members of the Gobiidae and Bleniidae.

3.2. Methods

3.2.1. Analysis of data for fish communities in nearshore, shallow waters derived from seine netting

The relationship between the means and standard deviations for the number of fish species, density and biomass per unit area derived from seine net samples collected on each sampling occasion from two sites at Port Smith, from two sites at Eighty Mile Beach and from one site at Cape Keraudren (see Table 2.1) were examined. This showed that, prior to analysis of variance (ANOVA), the first of these variables should be square-root transformed, while the last two should be $\log_{10}$ (n+1) transformed (see Clarke & Gorley (2001) for rationale for this approach).

The transformed values for the replicates for number of species, density and biomass of fish per unit area at each of the five sampling sites in each season were subjected to two-way ANOVA to determine whether these variables differed among sites and seasons. When ANOVA showed that the values for one or more of the main effects were significantly different and that there were no significant interactions between those effects, Scheffé's *a posteriori* test was used to determine which values were significantly different. Where there was a significant interaction between the main effects, the back-transformed mean values for these effects were plotted to elucidate the basis for the interaction.

The mean densities of the fish species in the seine net samples obtained from each site on each sampling occasion were ordinated using non-metric Multi-dimensional Scaling Ordination (nMDS), as described in the PRIMER v5 package (Clarke & Gorley,

2001). Prior to ordination, the densities were square-root transformed and the Bray-Curtis similarity measure used to produce the association matrix. One-way Analysis of Similarities (ANOSIM) was employed to test whether the species compositions in the different sampling sites and seasons were significantly different (Clarke, 1993). The R statistic values produced by the ANOSIM tests, where values approaching unity demonstrate that the compositions of the samples in each group are very different, while those close to zero show that they are very similar, were used to ascertain the degree to which the compositions at the different sites and in the different seasons were dissimilar and thus determine which variables were most important in contributing to any significant differences in community composition (Clarke, 1993). Note, however, that since, mainly due to severe weather, only one sample could be obtained for the early and late wet seasons at Cape Keraudren, the replicates were used to investigate the influence of season at this location.

ANOSIM was also employed to determine the degree to which the community composition at each site was influenced by the overall period. Separate "wet" and "dry" periods refer to a combination of early and late wet seasons and early and late dry seasons, respectively. Where appropriate, similarity percentages (SIMPER) were employed to determine which species typified samples from each overall location and which species were most responsible for any dissimilarities in the species composition of at each location (Clarke 1993). Similarly, SIMPER was also employed to determine which species, at each region, typified the various seasons and periods and which were most responsible for any differences in ichthyofaunal composition among seasons and between periods.

3.2.2. Analysis of data for fish communities in intertidal pools derived from rotenoning

The number of species collected in each pool satisfied the assumptions of ANOVA in an untransformed state. However, the density and biomass per unit area data were $\log_{10}$ (n+1) transformed prior to univariate analysis following the procedure outlined for the seine net samples.

The mean densities of the various fish species in the samples collected from intertidal pools using rotenone at Port Smith and Cape Keraudren were subjected to nMDS

ordination and associated tests in the same manner as described for the seine net data in Chapter 3.2.1. In addition to testing for the effect of season and period (*i.e*. wet vs dry) on the community composition of rotenone samples from Port Smith and Cape Keraudren, ANOSIM was also used to test if a severe tropical cyclone had an influence on the ichthyofauna of intertidal pools. Tropical Cyclone *Chris* crossed the north-western Australia coastline *ca* 25 km east of the study site at Cape Keraudren on the 5th of February 2002. Since sampling of intertidal pools was undertaken at Cape Keraudren *ca* 72 h after the cyclone crossed the coast, the community composition of three cyclone periods could be tested, *i.e*. immediately after the cyclone *vs* pre and post cyclone conditions. Pre-cyclone includes all samples collected >3 months prior to Cyclone *Chris* and post-cyclone includes all samples collected >3 months after Cyclone *Chris*.

As seine nets and rotenone were both employed at Port Smith and Cape Keraudren, the species composition of samples made with these two methods at these two regions were compared, based on species percentage contribution data, which were square-root transformed prior to the creation of the resemblance matrix. Samples were then ordinated and two-way crossed ANOSIM was employed to test whether the species compositions in the samples made using seine nets in shallow, nearshore waters and rotenone in intertidal pools at the two different sampling regions were significantly different (Clarke, 1993). Densities were not used for this comparison as the units for seine and rotenone data, *i.e.* number of individuals per 500 m^{-2} and 10 m^{-2}, respectively, were not comparable. Furthermore, the use of percentage contribution data facilitated a comparison of the composition of seine catches made over sand at Port Smith, Eighty Mile Beach and Cape Keraudren with that of gill net catches made in that habitat at the same locations (see Chapter 4). The degree of dispersion of the points representing the samples collected with seine nets and with rotenone was determined using the MVDISP routine in PRIMER v5 package (Clarke & Gorley, 2001).

3.3. Results

3.3.1. Environmental parameters

Mean water temperatures at Port Smith, Eighty Mile Beach and Cape Keraudren were highest during the early wet season, reaching 31.7, 31.6 and 28.5 °C, respectively (**Figure 3.1a**). Water temperatures then declined progressively to reach minima of 21.4 and 22.0 °C at Cape Keraudren and Port Smith during the early dry season and 23.7 °C at Port Smith during the late dry season (**Figure 3.1a**). Salinities at each of the three sampling locations did not depart markedly from that of full strength sea water with the maximum value of 37.4 ppt recorded at Eighty Mile Beach during the late dry season and the minimum of 33.8 ppt recorded at Port Smith during the late wet season (**Figure 3.1b**). Water clarity was greatest at Port Smith with secchi depth readings in excess of 2.0 m recorded throughout the year (**Figure 3.1c**). In contrast, secchi depths at Cape Keraudren and Eighty Mile Beach did not exceed 1.5 and 0.4 m, respectively (**Figure 3.1c**).

3.3.2. Species found in nearshore, shallow waters

A total of 36059 fish, representing 91 species and 39 families and weighing 319 kg, was caught using the 60.5 m seine net over bare sand at the two Port Smith sites, one of which was near mangroves, the two Eighty Mile Beach sites (northern and southern) and the Cape Keraudren site (**Table 3.1**). Twenty five of the 91 species were of commercial and recreational importance and these constituted 5.6% of the total catch of fish. A further 12 species, which were important only to the recreational sector, contributed a further 3.4% to the total catch. The most abundant species (and thus their percentage contributions to the total catch) were the engraulid *Stolephorus carpentariae* (19.1%), the clupeid *Herklotsichthys blackburni* (14.7%), the atherinids *Atherinomorus lacunosus* (11.8%) and *Craterocephalus capreoli* (8.7%), and another clupeid, *Spratelloides delicatulus* (7.8%). The only other species to contribute more than 5% to the total number of fish caught by the 60.5 m seine was the atherinid *Craterocephalus mugiloides* (7.7%) and another clupeid, *Herklotsichthys collettei* (5.4%). None of the above seven species are targeted by commercial or recreational fishers (**Table 3.1**).

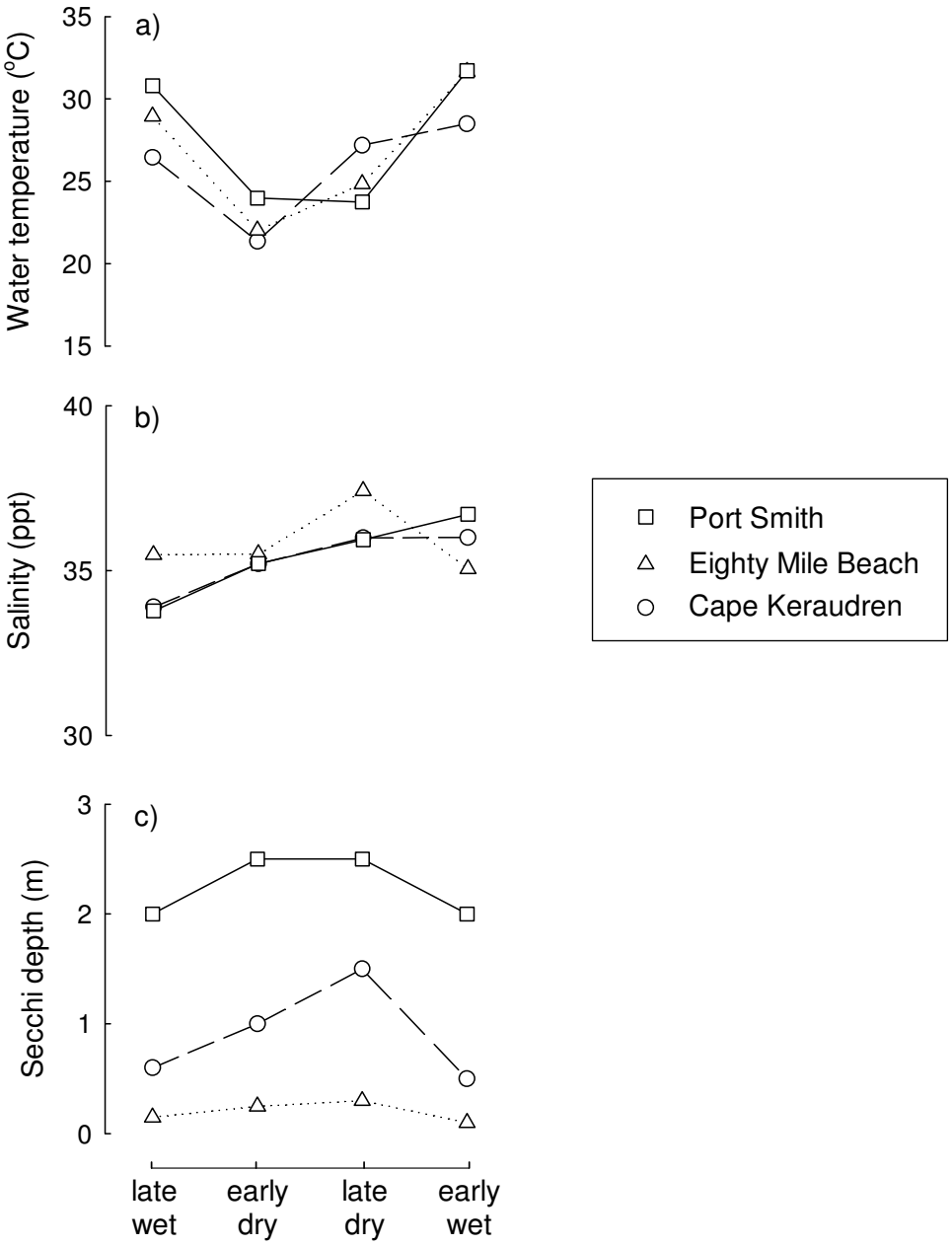

Figure 3.1. a) Mean water temperature, b) salinity and c) secchi depth values recorded at Cape Keraudren, Eighty Mile Beach and Port Smith in each season.

Table 3.1. Rank by abundance (R), number (N), percentage contribution by number (%) and length range of each fish species caught using the 60.5 m seine net over bare sand at Port Smith (2 sites), Eighty Mile Beach (2 sites) and Cape Keraudren (1 site). The ranking by weight, the total weight (g) and percentage contribution by weight of each species is also given. J, occurred as juveniles, A, occurred as adults; C, commercially fished; R, recreationally fished.

		Number			Numbers in each region					Weight					
		Total			Port Smith		Eighty Mile Beach		Cape Keraurdren	Total			Length Range	Life Cycle	Fisheries
Family	Species	R	N	%	North	South	North	South		R	g	%	(mm)		
Engraulididae	*Stolephorus carpentariae*	1	6895	19.1	1003	66	2	4	5820	6	13467.5	4.2	19 - 61	J, A	
Clupeidae	*Herklotsichthys blackburni*	2	5313	14.7	2981	1478	6	12	836	27	1871.4	0.6	23 - 132	J, A	
Atherinidae	*Atherinomorus lacunosus*	3	4241	11.8	483	3758				24	2447.8	0.8	20 - 75	J, A	
Atherinidae	*Craterocephalus capreoli*	4	3138	8.7	826	2297			15	28	1825.1	0.6	23 - 74	J, A	
Clupeidae	*Spratelloides delicatulus*	5	2808	7.8	1175	1633				30	1526.2	0.5	25 - 57	J, A	
Atherinidae	*Craterocephalus mugiloides*	6	2774	7.7	3	67	1		2703	18	3185.8	1.0	18 - 73	J, A	
Clupeidae	*Herklotsichthys collettei*	7	1956	5.4	817	1118			21	38	463.2	0.1	24 - 72	J, A	
Engraulididae	*Thryssa hamiltonii*	8	1402	3.9			227	1170	5	10	10263.5	3.2	23 - 273	J, A	
Leiognathidae	*Leiognathus equulus*	9	1203	3.3	791	402	7	3		48	178.4	<0.1	12 - 69	J, A	
Hemiramphidae	*Hyporhamphus quoyi*	10	977	2.7	60	81	67	719	50	14	5467.2	1.7	43 - 335	J, A	R
Sillaginidae	*Sillago vittata*	11	812	2.3	538	204		2	68	34	991.1	0.3	17 - 115	J	C,R
Clupeidae	*Escualosa thoracata*	12	706	2.0			462	236	8	35	984.5	0.3	22 - 78	J, A	
Gerreidae	*Gerres oyena*	13	485	1.3	357	111		1	16	49	160.3	<0.1	18 - 83	J, A	
Gerreidae	*Gerres subfasciatus*	14	472	1.3	117	337			18	43	271.5	<0.1	14 - 93	J, A	
Mugilidae	*Valamugil cunnesius*	15	404	1.1			25	347	32	7	13259.8	4.2	14 - 235	J, A	C,R
Engraulididae	*Stolephorus andhraensis*	16	342	0.9			25	307	10	40	352.7	0.1	32 - 95	J, A	
Polynemidae	*Eleutheronema tetradactylum*	17	277	0.8			76	199	2	5	16379.9	5.1	42 - 471	J, A	C,R
Chandidae	*Ambassis vachellii*	18	266	0.7		266				54	105.1	<0.1	15 - 60	J, A	
Sillaginidae	*Sillago lutea*	19	245	0.7		10	98	107	30	33	997.3	0.3	21 - 110	J	
Hemiramphidae	*Arrhamphus sclerolepis*	20	207	0.6		9	5	21	172	13	7299.8	2.3	35 - 240	J, A	R
Belonidae	*Strongylura strongylura*	21	189	0.5	20		18	55	96	11	10079.8	3.2	132 - 490	J, A	
Mugilidae	*Liza macrolepis*	22	143	0.4	1	10	1	1	130	8	11933.0	3.7	17 - 280	J, A	C,R
Engraulididae	*Thryssa setirostris*	23	104	0.3			53	51		50	145.8	<0.1	25 - 102	J, A	
Sillaginidae	*Sillago analis*	24	87	0.2	2		3	9	73	19	3041.0	1.0	24 - 295	J, A	C,R

Table 3.1. continued.

Family	Species	Number			Numbers in each region					Weight			Length Range (mm)	Life Cycle	Fisheries
		Total			Port Smith		Eighty Mile Beach		Cape Keraurdren	Total					
		R	N	%	North	South	North	South		R	g	%			
Polynemidae	*Polydactylus macrochir*	25	71	0.2			16	54	1	4	29975.6	9.4	147 - 576	J, A	C,R
Sillaginidae	*Sillago burrus*	26	36	<0.1	17	5			14	55	90.2	<0.1	31 - 112	J	C,R
Mugilidae	*Liza subviridis*	27	33	<0.1			1	1	31	17	3870.2	1.2	127 - 317	J, A	C,R
Leiognathidae	*Secutor insidiator*	28	32	<0.1	13	4	9	6		60	62.7	<0.1	12 - 69	J, A	
Sciaenidae	*Nibea microgenys*	29"	29	<0.1			3	26		15	4419.2	1.4	189 - 382	J, A	C,R
Pleuronectidae	*Psammodiscus ocellatus*	29"	29	<0.1	22	7				67	14.6	<0.1	17 - 73	J	
Leptobramidae	*Leptobrama mulleri*	31"	25	<0.1			3	6	16	29	1636.8	0.5	130 - 255	J, A	
Engraulididae	*Thryssa aestuaria*	31"	25	<0.1			7	18		46	209.8	<0.1	46 - 138	J, A	
Cynoglossidae	*Paraplagusia bilineata*	33	24	<0.1			20	4		62	45.0	<0.1	27 - 140	J	
Carangidae	*Scomberoides commersonnianus*	34	23	<0.1	4	6	1	5	7	25	2346.6	0.7	23 - 207	J	C,R
Teleost	juvenile teleost F	35	20	<0.1			16	4		75	4.5	<0.1	18 - 29	J	
Mugilidae	*Liza vaigiensis*	36	19	<0.1		15			4	21	2993.6	0.9	15 - 450	J, A	C,R
Tetraodontidae	*Arothron manilensis*	37"	15	<0.1	9	2	1	1	2	26	1937.1	0.6	117 - 183	A	
Dasyatididae	*Himantura undulata*	37"	15	<0.1			3	10	2	1	53500.0	16.8	200 - 700	J, A	
Carangidae	*Caranx ignobilis*	39	14	<0.1			2		12	51	137.6	<0.1	62 - 167	J	C,R
Dasyatididae	*Pastinachus sephen*	40	13	<0.1			1	9	3	2	39500.0	12.4	350 - 650	J, A	
Atherinidae	*Craterocephalus pauciradiatus*	41"	11	<0.1			1	10		73	6.1	<0.1	30 - 56	J, A	
Platycephalidae	*Platycephalus endrachtensis*	41"	11	<0.1	6	5				59	65.5	<0.1	38 - 152	J, A	R
Mugilidae	*Valamugil buchanani*	43	10	<0.1	2	4			4	32	1130.7	0.4	95 - 318	J, A	C,R
Carangidae	*Scomberoides tol*	44"	9	<0.1	4	1			4	58	68.2	<0.1	28 - 141	J	R
Engraulididae	*Stolephorus nelsoni*	44"	9	<0.1			2	5	2	74	5.9	<0.1	45 - 56	J, A	
Carangidae	*Caranx sexfasciatus*	46"	8	<0.1			2	5	1	42	294.6	<0.1	72 - 220	J	C,R
Hemiramphidae	*Hyporhamphus neglectisimus*	46"	8	<0.1			4	1	3	71	10.4	<0.1	41 - 122	J, A	

Table 3.1. continued.

Family	Species	Number			Numbers in each region					Weight			Length Range	Life Cycle	Fisheries
		Total			Port Smith		Eighty Mile Beach		Cape Keraurdren	Total					
		R	N	%	North	South	North	South		R	g	%	(mm)		
Lutjanidae	*Lutjanus russelli*	46"	8	<0.1		2	5	1		77	3.2	<0.1	28 - 34	J	C,R
Paralichthyidae	*Pseudorhombus arsius*	46"	8	<0.1	8					76	3.4	<0.1	21 - 42	J	R
Carangidae	*Trachinotus blochii*	46"	8	<0.1	8					9	11200.0	3.5	460 - 460	A	R
Gobiidae	*Favonigobius lateralis*	51"	7	<0.1			4	3		78	1.3	<0.1	27 - 31	J, A	
Rhinobatidae	*Rhinobatos typus*	51"	7	<0.1	1		2	2	2	12	9800.0	3.1	400 - 700	J	C,R
Sillaginidae	*Sillago sihama*	53	6	<0.1				3	3	63	29.0	<0.1	86 - 98	J	C,R
Mugilidae	*Liza planiceps*	54"	5	<0.1					5	52	116.4	<0.1	144 - 164	J, A	C,R
Clupeidae	*Nematalosa come*	54"	5	<0.1			2	3		61	58.8	<0.1	38 - 133	J, A	
Polynemidae	*Polydactylus multiradiatus*	54"	5	<0.1			1	4		39	362.0	0.1	180 - 203	J, A	
Ariidae	*Arius proximus*	54"	5	<0.1				5		23	2503.0	0.8	252 - 436	A	C,R
Teraponidae	*Terapon jarbua*	58"	4	<0.1					4	64	27.6	<0.1	64 - 98	J	
Ariidae	*Arius mastersi*	58"	4	<0.1			1	3		22	2873.5	0.9	116 - 507	A	C,R
Teleost	juvenile teleost D	58"	4	<0.1			1	3		84"	0.3	<0.1	16 - 17	J	
Gerreidae	*Gerres filamentosus*	61"	3	<0.1		3				68	14.0	<0.1	67 - 73	J, A	
Hemiramphidae	*Hyporhamphus affinis*	61"	3	<0.1	1	1	1			66	14.7	<0.1	38 - 157	J, A	R
Pristidae	*Pristis zijsron*	61"	3	<0.1					3	3	32000.0	10.0	1000 - 1500	J	C,R
Sphyraenidae	*Sphyraena qenie*	61"	3	<0.1			1	2		80"	0.6	<0.1	31 - 37	J	R
Teraponidae	*Amniataba caudavittatus*	65"	2	<0.1		2				65	18.6	<0.1	86 - 88	J	
Drepanidae	*Drepane punctata*	65"	2	<0.1		1		1		41	351.3	0.1	123 - 250	J, A	
Mugilidae	*Mugil cephalus*	65"	2	<0.1				1	1	36	688.5	0.2	134 - 402	J, A	C,R
Mugilidae	*Rhinomugil nasutus*	65"	2	<0.1				2		45	220.9	<0.1	210 - 236	J, A	
Scatophagidae	*Selenotoca multifasciata*	65"	2	<0.1	1			1		53	114.6	<0.1	45 - 181	J, A	
Belonidae	*Strongylura incisa*	65"	2	<0.1	2					72	8.0	<0.1	150 - 155	J	
Ariidae	*Arius argyropleuron*	65"	2	<0.1				2		31	1342.5	0.4	354 - 453	A	C,R

Table 3.1. continued.

Family	Species	Number			Numbers in each region					Weight			Length Range (mm)	Life Cycle	Fisheries
		Total			Port Smith		Eighty Mile Beach		Cape Keraurdren	Total					
		R	N	%	North	South	North	South		R	g	%			
Ariidae	*Arius* cf *nella*	65"	2	<0.1				2		37	628.7	0.2	246 - 376	A	C,R
Teleost	juvenile teleost G	65"	2	<0.1				2		91	0.0	<0.1	9 - 10	J	
Chanidae	*Chanos chanos*	74"	1	<0.1		1				47	196.9	<0.1	290	J	R
Elopidae	*Elops hawaiensis*	74"	1	<0.1					1	44	237.5	<0.1	356	J	R
Dasyatididae	*Himantura fai*	74"	1	<0.1					1	16	4000.0	1.3	600	A	
Haemulidae	*Pomadasys kaakan*	74"	1	<0.1					1	80"	0.6	<0.1	37	J	R
Eceneidae	*Remora remora*	74"	1	<0.1				1		69	13.7	<0.1	172	J	
Soleidae	*Rendahlia jaubertensis*	74"	1	<0.1			1			84"	0.3	<0.1	32	J	
Monocanthidae	*Scobinichthys granulatus*	74"	1	<0.1			1			82	0.6	<0.1	31	J	R
Scombridae	*Scomberomorus* sp	74"	1	<0.1				1		84"	0.3	<0.1	35	J	
Triacanthidae	*Tripodichthys angustifrons*	74"	1	<0.1	1					56	84.4	<0.1	211	A	
Belonidae	*Tylosurus crocodilus*	74"	1	<0.1		1				70	11.8	<0.1	213	J	
Teleost	juvenile teleost A	74"	1	<0.1			1			87"	0.1	<0.1	16	J	
Teleost	juvenile teleost B	74"	1	<0.1			1			87"	0.1	<0.1	18	J	
Teleost	juvenile teleost C	74"	1	<0.1			1			87"	0.1	<0.1	24	J	
Teraponidae	tetraodontid sp1	74"	1	<0.1		1				90	0.1	<0.1	12	J	
Mullidae	*Upeneus tragula*	74"	1	<0.1	1					83	0.5	<0.1	37	J	
Dasyatididae	*Urogymnus asperrimus*	74"	1	<0.1				1		20	3000.0	0.9	500	A	
Mugilidae	*Valamugil perusii*	74"	1	<0.1					1	57	68.9	<0.1	183	A	C,R
Hemiramphidae	*Zenarchopterus buffonis*	74"	1	<0.1		1				79	1.0	<0.1	81	J?	
	Total fish		36059		9274	11909	1190	3452	10233						
	Number of species		91		30	34	47	53	44						
	Total biomass (kg)		319.0		18.8	15.0	24.8	142.4	118.1						

Although these seven abundant species collectively contributed more than 75% to the total number of fish caught by the 60.5 m seine over bare sand, only 25 individuals of these species collectively were caught at the two Eighty Mile Beach sites and thus contributed only 0.5% to the total number of fish at those sites. This low number helps account for the total number of fish at both of these sites (1190 and 3452) being far lower than at either of the Port Smith sites (9274 and 11909) or Cape Keraudren (10233). In contrast, the total number of species recorded over bare sand was greater at each of the two Eighty Mile Beach sites (47 and 53) than that at Cape Keraudren (44) and even more particularly at the sites at Port Smith (30 and 34) (**Table 3.1**). The contribution of commercially and/or recreationally important species to the total catch of fish in each location ranged from 2.9% at the southern Port Smith site to 40.8% at the southern Eighty Mile Beach site (**Table 3.1**).

The Spotted Whipray *Himantura undulata* made the greatest contribution (16.8%) to the total biomass of fish collected by seine netting, followed by the Cowtail Stingray *Pastinachus sephen* (16.8%) and the Green Sawfish *Pristis zijsron* (10.0%) (**Table 3.1**). Although these three elasmobranch species collectively contributed 39.5% to the total biomass, none of them ranked higher than 37th or contributed more than 0.1% in terms of the total number of fish caught with the seine net. The next ranked species in terms of biomass were the threadfins *P. macrochir* (9.4%) and *E. tetradactylum* (5.1%). In contrast to their low contribution to the total number of individuals, the species of commercial and recreational significance constituted 140.9 kg (44.2%) of the total weight of the seine net catch, with those species important only to recreational fishers contributing a further 24.6 kg (7.7%).

3.3.3. Number of species, densities and biomass of fish in nearshore, shallow waters

ANOVA of the number of species caught in replicate samples by seine netting over bare sand at the two sites at both Port Smith and Eighty Mile Beach and at the Cape Keraudren site on each sampling occasion in the different seasons showed that the number of species differed significantly ($p<0.001$) among those sites but not among seasons (**Table 3.2**). The density and biomass of fish were both significantly influenced by site and season ($p<0.05$

Table 3.2. Mean squares and significance levels for ANOVAs of the number of species, density and biomass per unit area over bare sand in nearshore shallow waters at two sites at both Port Smith and Eighty Mile Beach and at one site at Cape Keraudren in each season. *** $p<0.001$, * $p<0.05$

	Main effects		Interactions	
Source	Site (St)	Season (Sn)	St x Sn	Residual
Degrees of freedom	4	3	12	79
Number of species	3.07 ***	0.39	0.42	0.34
Density (500 m^{-1})	1.58 *	1.57 *	0.25	0.48
Biomass (500 m^{-1})	3.99 ***	1.62 *	0.97 *	0.51

or p<0.001) and there was a significant interaction between those two variables in the case of biomass.

The mean number of species at the northern Eighty Mile Beach site (8.1) and southern Eighty Mile Beach site (9.2) were both significantly greater ($p<0.01$) than at the northern and southern sites at Port Smith (4.4 and 5.5 species, respectively). Similarly, the mean number of species at the Cape Keraudren site (8.2) was also significantly greater ($p<0.05$) than at the bare sand site at Port Smith (**Figure 3.2a**). The mean densities of fish at the five sites sampled with the seine net ranged from 54.7 fish 500 m^{-2} at the northern Eighty Mile Beach site to 259.7 fish 500 m^{-2} at the southern Port Smith site (**Figure 3.2b**). The mean density of fish during the early dry season (212.1 fish 500 m^{-2}) was significantly greater than during the late dry season (52.5 fish 500 m^{-2}) (**Figure 3.2c**). The biomass of fish at Cape Keraudren declined from a high of 8.2 kg 500 m^{-2} during the late wet season to a low of 0.6 kg 500 m^{-2} during the late dry season, before increasing to 3.4 kg 500 m^{-2} during the early wet season (**Figure 3.2d**). In contrast, the biomass at both the northern and southern Eighty Mile Beach sites increased between the late wet and early dry seasons, reaching 1.9 and 6.7 kg 500 m^{-2}, respectively, before declining progressively to a minimum of approximately 0.3 kg 500 m^{-2} during the early wet. The biomass of fish at both Port Smith sites remained relatively constant, never exceeding 1.3 kg 500 m^{-2} during any season (**Figure 3.2d**).

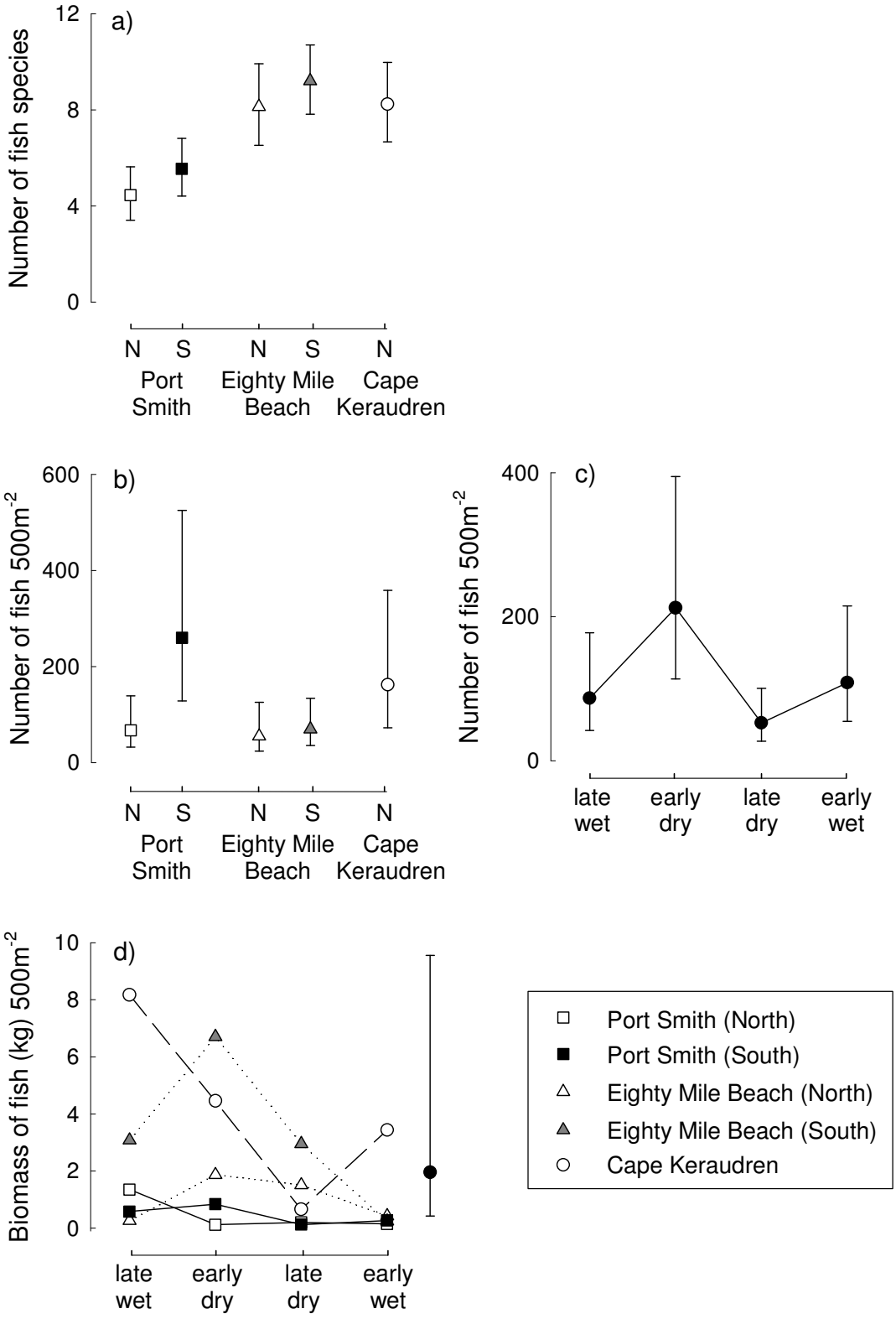

Figure 3.2. a) Mean number of fish species ± 95% CL, b,c) mean number of fish 500 m^{-2} ± 95% CL and d) mean biomass of fish 500 m^{-2} ± 95% CL collected with the seine net over bare sand at sites at Port Smith, Eighty Mile Beach and Cape Keraudren in each season. In this Figure and Figure 3.5 a common mean and 95% CL is shown when there are significant interactions between the main effects.

3.3.4. Species composition of fish in nearshore, shallow waters

When the mean densities of the various species over bare sand at the five sites on the different sampling occasions were subjected to nMDS ordination, the samples from the northern and southern Eighty Mile Beach sites formed a discrete group in the top right hand corner of the plot (**Figure 3.3**). All but one of the samples from the Port Smith sites formed a tight and discrete group in the top left hand corner of the ordination plot. The samples from Cape Keraudren formed a separate group that lay largely between and below those from Eighty Mile Beach and Port Smith (**Figure 3.3**).

A one-way ANOSIM confirmed that the compositions of the fish fauna at the five sites were significantly different ($p<0.001$, Global R-statistic = 0.715). Pairwise ANOSIM tests revealed that the composition of the fish fauna at the northern site at Port Smith did not differ significantly from that at the southern Port Smith site and neither were there significant differences between the compositions of the fish faunas at the two sites at Eighty Mile Beach. However, the faunal composition did differ significantly between sites in the different locations, *i.e.* between Port Smith, Eighty Mile Beach and Cape Keraudren, with $p<0.01$ or $p<0.001$ in each case, and the R-statistic of 0.993 being greatest for the comparison between the southern Eighty Mile Beach site and the southern Port Smith site (**Table 3.3**).

Table 3.3. R-statistic values and significance levels for pair-wise ANOSIM tests comparing the fish community composition at each of the five sites sampled with the 60.5 m seine net at Port Smith, Eighty Mile Beach and Cape Keraudren. *** $p<0.001$, ** $p<0.01$

	Port Smith North	Port Smith South	Eighty Mile Beach North	Eighty Mile Beach South
Port Smith South	0.003			
Eighty Mile Beach North	0.949 ***	0.974 **		
Eighty Mile Beach South	0.961 **	0.993 **	0.030	
Cape Keraudren	0.725 ***	0.868 **	0.905 ***	0.953 **

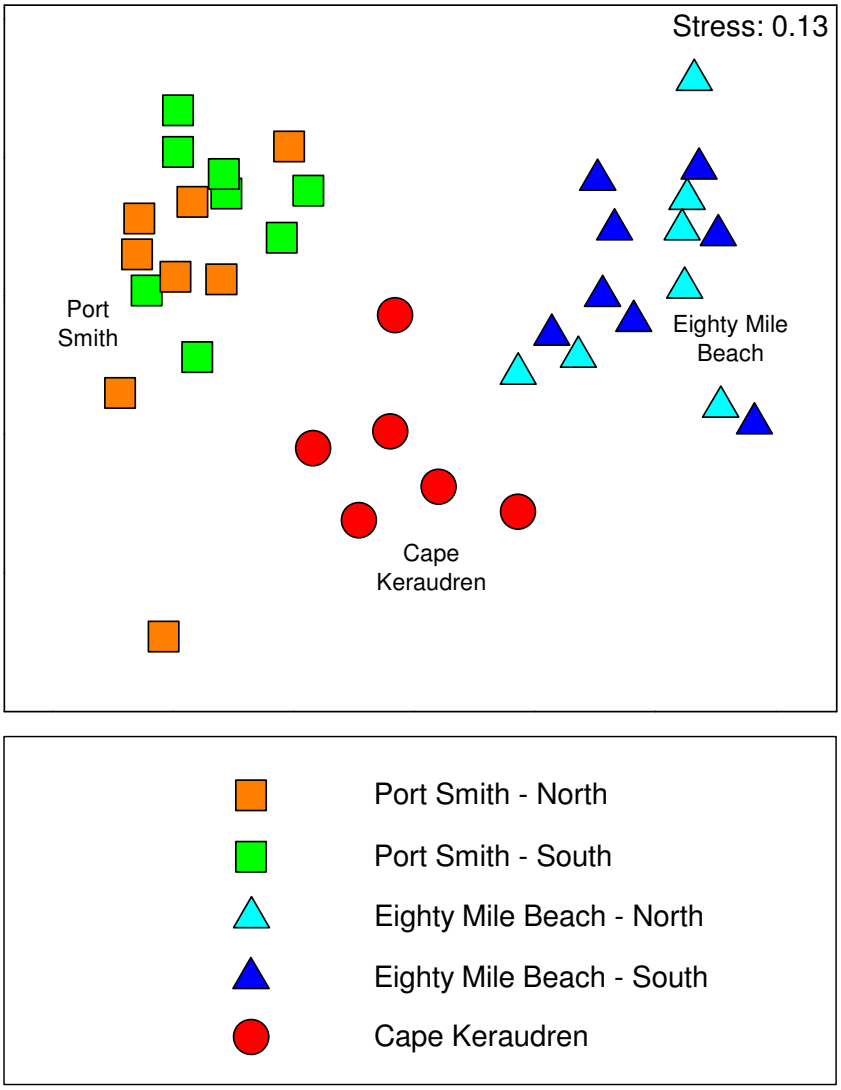

Figure 3.3. Nonmetric multidimensional scaling ordination of the mean catch rates of the various species in samples collected with the seine net on each sampling occasion over bare sand at two sites at both Port Smith and Eighty Mile Beach and one site at Cape Keraudren.

SIMPER demonstrated that the community composition of seine net samples collected at Port Smith, Eighty Mile Beach and Cape Keraudren were distinguished from one another by relatively greater numbers of *Craterocephalus capreoli* at the two Port Smith sampling sites, by *Escualosa thoracata,* and *Thryssa hamiltonii* at the two Eighty Mile Beach sites and *Craterocephalus mugiloides* and *Arrhamphus sclerolepis* at Cape Keraudren (**Table 3.4**).

When the mean densities of the various fish species at Port Smith were subjected to ordination, the samples from each of the four seasons formed groups that progressed cyclically in a clockwise direction (**Figure 3.4a**). Thus, samples from the early dry season are located toward the lower centre part of the plot, directly below those for the late dry season and to the left of those from the early wet season, which are located above three of the four samples from the late wet season in the bottom right of the plot (**Figure 3.4a**).

ANOSIM revealed that the faunal composition at Port Smith was significantly influenced by season ($p<0.01$, Global R-statistic = 0.486) (**Table 3.5**). The greatest seasonal difference ($p<0.05$, R-statistic = 0.854) was that recorded between the early dry and early wet seasons (**Table 3.6**). SIMPER showed that seine net samples at Port Smith collected during the early dry season were distinguished from the late dry season and the early wet season by higher numbers of *Hyporhamphus quoyi* and *S. delicatulus,* whereas the early wet season was distinguished from the early and late dry seasons by relatively higher numbers of *Psammodiscus ocellatus Gerres subfasciatus* and *H. blackburni* (**Table 3.7**). The late wet season was distinguished from the early wet season by relatively higher numbers of *H. quoyi, A. lacunosus* and *Leiognathus equulus* and fewer *P. ocellatus G. subfasciatus* and *Sillago vittata.*

ANOSIM also demonstrated that, in addition to being influenced by season, the fish fauna at Port Smith was also influenced by period, *i.e.* wet *vs* dry ($p<0.05$, R-statistic = 0.155) (**Table 3.5**). SIMPER showed that the difference in community composition between the wet and dry periods was due to the presence of relatively greater numbers of *G. subfasciatus, A. lacunosus* and *H. blackburni* during the former period and greater numbers of *H. quoyi* during the latter period (**Table 3.8**).

Table 3.4. Species identified by SIMPER as those that typified the fish assemblages over bare sand at two sites at both Port Smith and Eighty Mile Beach and one site at Cape Keraudren (shaded boxes) and distinguished between the fish assemblages at each pair of those locations (non-shaded boxes). For each pair-wise comparison between locations, the species that distinguish between the fauna at one location from that at another location are indicated by the initials of that location.

	Port Smith North	Port Smith South	Eighty Mile Beach North	Eighty Mile Beach South	Cape Keraudren
Port Smith North	*Sillago vittata* *Craterocephalus capreoli* *Hyporhamphus quoyi* *Atherinomorus lacunosus*				
Port Smith South	*ns*	*Craterocephalus capreoli* *Atherinomorus lacunosus* *Sillago vittata* *Gerres subfasciatus*			
Eighty Mile Beach North	*C. capreoli* PSM *Sillago vittata* PSM *Escualosa thoracata* EMN *Thryssa hamiltonii* EMN *Valamugil cunnesius* EMN	*C. capreoli* PSM *Escualosa thoracata* EMN *Thryssa hamiltonii* EMN *Atherinomorus lacunosus* PSM *Gerres subfasciatus* PSM	*Escualosa thoracata* *Thryssa hamiltonii* *Valamugil cunnesius* *Polydactylus macrochir*		
Eighty Mile Beach South	*Escualosa thoracata* EMS *E. tetradactylum* EMS *C. capreoli* PSS *Polydactylus macrochir* EMS *Sillago vittata* PSS *Thryssa hamiltonii* EMS	*Escualosa thoracata* EMS *E. tetradactylum* EMS *C. capreoli* PSM *Thryssa hamiltonii* EMS *Atherinomorus lacunosus* PSM *Valamugil cunnesius* EMS	*ns*	*Escualosa thoracata* *Thryssa hamiltonii* *Eleutheronema tetradactylum* *Polydactylus macrochir* *Valamugil cunnesius*	
Cape Keraudren	*Craterocephalus mugiloides* CK *Arrhamphus sclerolepis* CK *Sillago analis* CK *C. capreoli* PSS	*Craterocephalus mugiloides* CK *Sillago analis* CK *C. capreoli* PSM *Arrhamphus sclerolepis* CK *Atherinomorus lacunosus* PSM	*Craterocephalus mugiloides* CK *Sillago analis* CK *Arrhamphus sclerolepis* CK *Escualosa thoracata* EMN *Thryssa hamiltonii* EMN	*Craterocephalus mugiloides* CK *E. tetradactylum* EMN *Polydactylus macrochir* EMN *Escualosa thoracata* EMN *Arrhamphus sclerolepis* CK	*Craterocephalus mugiloides* *Arrhamphus sclerolepis* *Sillago analis*

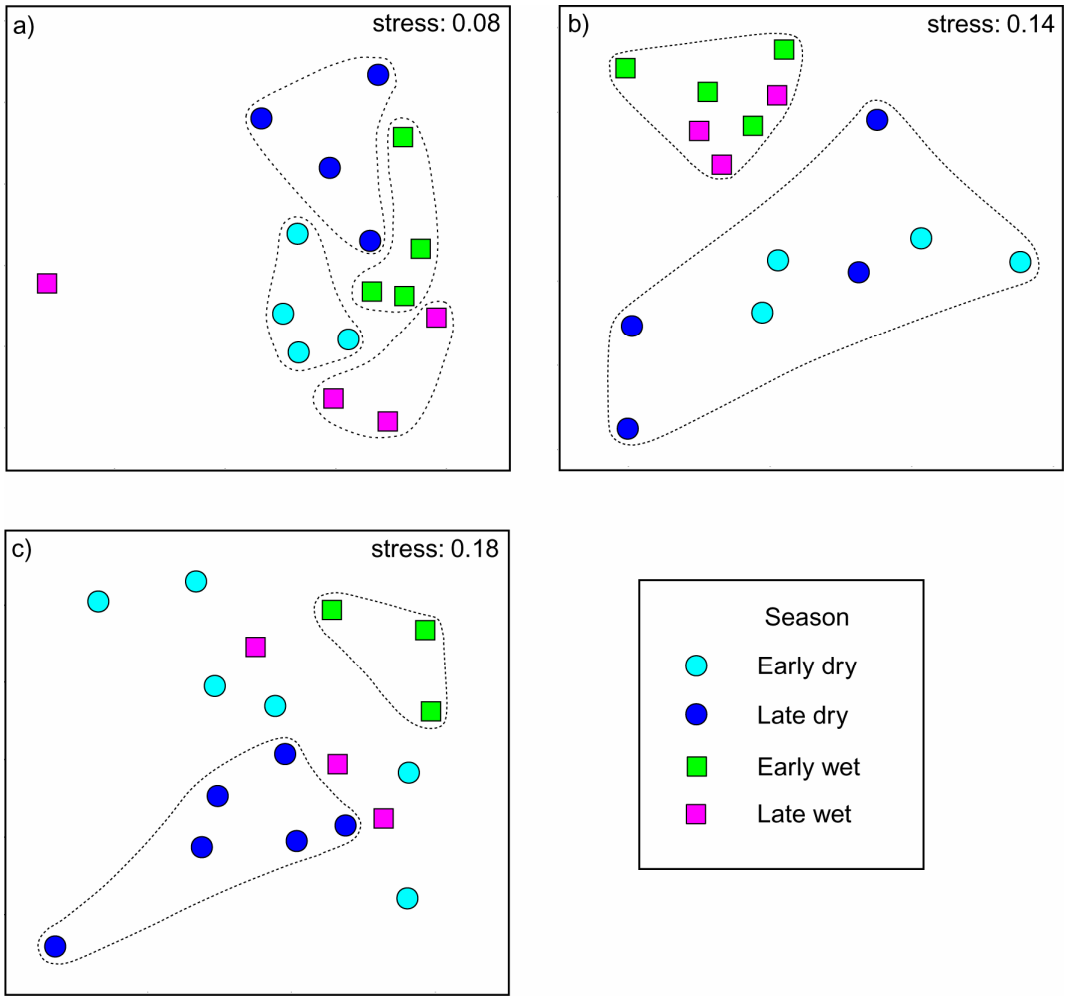

Figure 3.4. Nonmetric multidimensional scaling ordination of the mean catch rates of the various species in samples collected with the seine net at a) Port Smith and b) Eighty Mile Beach and c) the replicate catch rates of the various species in samples collected with the seine net at and Cape Keraudren on each sampling occasion.

Table 3.5. R-statistic values and significance levels for one-way ANOSIM tests for the effect of season and period (*i.e.* wet vs dry) on the fish fauna collected with seine nets over bare sand at Port Smith, Eighty Mile Beach and Cape Keraudren.
*** $p<0.001$, ** $p<0.01$

	Port Smith	Eighty Mile Beach	Cape Keraudren
Season	0.486 ***	0.409 **	0.433 ***
Period	0.155 *	0.507 ***	0.189 *

Table 3.6. R-statistic values and significance levels for pair-wise ANOSIM tests comparing the community composition during each of the four seasons sampled using mean density data of fish collected with the 60.5 m seine net at Port Smith. * $p<0.05$

	Early dry	Late dry	Early wet
Late dry	0.521 *		
Early wet	0.854 *	0.396 *	
Late wet	0.344	0.385	0.542 *

Table 3.7. Species identified by SIMPER as typifying the fish samples caught in each season with the 60.5 m seine net in shallow, nearshore waters at Port Smith (shaded boxes) and those that distinguished between the fish assemblages in each season (non-shaded boxes). For the pair-wise comparisons between seasons, the species that distinguish the fauna of one season from that of another are indicated by the initials of that season.

	Early dry	Late dry	Early wet	Late wet
Early dry	*Craterocephalus capreoli* *Atherinomorus lacunosus* *Spratelloides delicatulus* *Hyporhamphus quoyi* *Sillago vittata*			
Late dry	*Hyporhamphus quoyi* ED *Sillago vittata* LD *Atherinomorus lacunosus* ED *Sillago burrus* LD *Craterocephalus capreoli* ED *Spratelloides delicatulus* ED	*Sillago vittata* *Craterocephalus capreoli* *Herklotsichthys collettei* *Sillago burrus*		
Early wet	*Hyporhamphus quoyi* ED *Psammodiscus ocellatus* EW *Gerres subfasciatus* EW *Sillago vittata* EW *Herklotsichthys blackburni* EW *Spratelloides delicatulus* ED	*Atherinomorus lacunosus* EW *Psammodiscus ocellatus* EW *Herklotsichthys blackburni* EW *Craterocephalus capreoli* EW *Gerres subfasciatus* EW	*Craterocephalus capreoli* *Sillago vittata* *Herklotsichthys blackburni* *Gerres subfasciatus* *Atherinomorus lacunosus* *Psammodiscus ocellatus*	
Late wet	*ns*	*ns*	*Hyporhamphus quoyi* LW *Atherinomorus lacunosus* LW *Leiognathus equulus* LW *Gerres subfasciatus* EW *Psammodiscus ocellatus* EW *Sillago vittata* EW	*Hyporhamphus quoyi* *Atherinomorus lacunosus* *Craterocephalus capreoli* *Leiognathus equulus* *Stolephorus carpentariae*

Table 3.8. Species identified by SIMPER as typifying (shaded boxes) the fish assemblages in each period, *i.e.* dry *vs*, wet in shallow, nearshore waters at Port Smith and those that distinguished between the fish assemblages in each period (non-shaded box). For the pair-wise comparisons between periods, the species that distinguish the fauna of one period from that of another are indicated by the initials of that period.

	Dry	Wet
Dry	*Craterocephalus capreoli* *Sillago vittata* *Atherinomorus lacunosus* *Hyporhamphus quoyi* *Spratelloides delicatulus*	
Wet	*Gerres subfasciatus* W *Hyporhamphus quoyi* D *Atherinomorus lacunosus* W *Herklotsichthys blackburni* W	*Craterocephalus capreoli* *Atherinomorus lacunosus* *Herklotsichthys blackburni* *Sillago vittata* *Gerres subfasciatus*

When the densities for the various species in samples from Eighty Mile Beach were subjected to nMDS ordination, the samples from both the early and late wet seasons formed a relatively tight group in the top left-hand corner of the ordination plot, whereas all but one of those from both the early and late dry seasons were located in the bottom half of the plot (**Figure 3.4b**). ANOSIM confirmed that the faunal composition at Eighty Mile Beach was significantly influenced by season ($p<0.01$, Global R-statistic = 0.409) and that the composition in the early wet season differed significantly from that in both the early and late dry seasons while that in the late wet season differed from that in the early dry season (**Table 3.9**).

Table 3.9. R-statistic values and significance levels for pair-wise ANOSIM tests comparing the community composition during each of the four seasons sampled with the 60.5 m seine net at Eighty Mile Beach. * $p<0.05$

	Early dry	Late dry	Early wet
Late dry	0.188		
Early wet	0.771 *	0.448 *	
Late wet	0.741 *	0.259	-0.037

SIMPER revealed that the community composition during the early wet season was distinguished from that of the early dry season by relatively greater numbers of *Valamugil cunnesius* and *T. setirostris* during the former season and large numbers of *H. quoyi* during the latter season (**Table 3.10**). *Thryssa setirostris* also distinguished the community composition of the early wet season from that of the late dry season. The difference in community composition between the late wet season and the early dry seasons could be attributed to relatively greater numbers of *V. cunnesius* during the late wet season and *Strongylura strongylura* during the early dry season (**Table 3.10**).

ANOSIM also demonstrated that the fish fauna at Eighty Mile Beach was strongly influenced by period, *i.e.* wet *vs* dry ($p<0.001$, R-statistic = 0.468) (**Table 3.5**). SIMPER showed that the difference in community composition between the wet and dry periods was due to the presence of relatively greater numbers of *T. setirostris* and *V. cunnesius* during the former period and greater numbers of *S. strongylura* and *E. thoracata* during the latter period (**Table 3.11**).

When the densities of the various species, derived from replicate samples at Cape Keraudren, were subjected to nMDS ordination, the samples from the late dry season lay towards the bottom left hand corner of the plot and were separated from the early wet samples in the top right hand corner by those for the samples for the early dry season and late wet season (**Figure 3.4c**). A one-way ANOSIM performed on replicate data revealed that the community composition at Cape Keraudren was significantly influenced by season ($p<0.01$, Global R-statistic = 0.433) (**Table 3.5**). Pairwise ANOSIM tests further revealed that the community composition differed significantly between each season ($p<0.05$ or $p<0.01$), except in the case of late wet *vs* late dry and late wet *vs* early wet (**Table 3.12**). Seine net samples typically contained relatively greater numbers of *Liza subviridis* in the early dry season than each of the other seasons, while the community composition of early wet season samples was distinguished from both the early and late dry seasons by *Gerres oyena*, *H. blackburni* and *C. capreoli* (**Table 3.13**).

ANOSIM also demonstrated that the fish fauna at Cape Keraudren was influenced by period, *i.e.* wet *vs* dry ($p<0.05$, R-statistic = 0.189) (**Table 3.5**). SIMPER showed that the difference in community composition between the wet and dry periods was due to the

Table 3.10. Species identified by SIMPER as typifying the fish samples caught in each season with the 60.5 m seine net in shallow, nearshore waters at Eighty Mile Beach (shaded boxes) and those that distinguished between the fish assemblages in each season (non-shaded boxes). For the pair-wise comparisons between seasons, the species that distinguish the fauna of one season from that of another are indicated by the initials of that season.

	Early dry	Late dry	Early wet	Late wet
Early dry	*Hyporhamphus quoyi* *Thryssa hamiltonii* *Escualosa thoracata* *Polydactylus macrochir* *Valamugil cunnesius*			
Late dry	*ns*	*Escualosa thoracata* *Strongylura strongylura* *Paraplagusia bilineata* *Valamugil cunnesius* *Eleutheronema tetradactylum*		
Early wet	*Valamugil cunnesius* EW *Thryssa setirostris* EW *Hyporhamphus quoyi* ED *Strongylura strongylura* ED *Escualosa thoracata* ED	*Thryssa setirostris* EW *Thryssa hamiltonii* EW *Eleutheronema tetradactylum* EW *Strongylura strongylura* LD	*Thryssa hamiltonii* *Escualosa thoracata* *Thryssa setirostris* *Valamugil cunnesius* *Eleutheronema tetradactylum*	
Late wet	*Valamugil cunnesius* LW *Strongylura strongylura* ED *Hyporhamphus quoyi* ED *Escualosa thoracata* ED *Thryssa setirostris* LW	*ns*	*ns*	*Thryssa hamiltonii* *Escualosa thoracata* *Eleutheronema tetradactylum* *Valamugil cunnesius* *Thryssa setirostris*

Table 3.11. Species identified by SIMPER as typifying (shaded boxes) the fish assemblages in each period, *i.e.* dry *vs*, wet in shallow, nearshore waters at Eighty Mile Beach and those that distinguished between the fish assemblages in each period (non-shaded box). For the pair-wise comparisons between periods, the species that distinguish the fauna of one period from that of another are indicated by the initials of that period.

	Dry	Wet
Dry	*Escualosa thoracata* *Strongylura strongylura* *Polydactylus macrochir* *Thryssa hamiltonii* *Eleutheronema tetradactylum*	
Wet	*Thryssa setirostris* W *Strongylura strongylura* D *Valamugil cunnesius* W *Escualosa thoracata* D *Thryssa hamiltonii* W	*Thryssa hamiltonii* *Escualosa thoracata* *Valamugil cunnesius* *Thryssa setirostris* *Eleutheronema tetradactylum*

Table 3.12. R-statistic values and significance levels for pair-wise ANOSIM tests comparing the community composition during each of the four seasons sampled with the 60.5 m seine net at Cape Keraudren. ** $p<0.01$, * $p<0.05$

	Early dry	Late dry	Early wet
Late dry	0.419 **		
Early wet	0.438 *	0.667 *	
Late wet	0.352 *	0.290	0.667

Table 3.13. Species identified by SIMPER as typifying the fish samples caught in each season with the 60.5 m seine net in shallow, nearshore waters at Cape Keraudren (shaded boxes) and those that distinguished between the fish assemblages in each season (non-shaded boxes). For the pair-wise comparisons between seasons, the species that distinguish the fauna of one season from that of another are indicated by the initials of that season.

	Early dry	Late dry	Early wet	Late wet
Early dry	*Craterocephalus mugiloides* *Stolephorus carpentariae* *Liza subviridis* *Arrhamphus sclerolepis* *Sillago analis*			
Late dry	*Liza subviridis* ED *Craterocephalus mugiloides* ED *Sillago analis* ED *Arrhamphus sclerolepis* LD	*Craterocephalus mugiloides* *Arrhamphus sclerolepis* *Hyporhamphus quoyi*		
Early wet	*Gerres oyenya* EW *Liza subviridis* ED *Herklotsichthys blackburni* EW *Craterocephalus capreoli* EW	*Gerres oyenya* EW *Sillago analis* EW *Craterocephalus mugiloides* EW *Herklotsichthys blackburni* EW *Craterocephalus capreoli* EW	*Craterocephalus mugiloides* *Sillago analis* *Gerres oyenya* *Herklotsichthys blackburni*	
Late wet	*Liza subviridis* ED *Craterocephalus mugiloides* LW *Sillago analis* ED *Strongylura strongylura* ED *Caranx ignobilis* LW	*ns*	*ns*	*Craterocephalus mugiloides* *Arrhamphus sclerolepis*

presence of relatively greater numbers of *C. mugiloides* and *S. strongylura* during the wet period (**Table 3.14**).

Table 3.14. Species identified by SIMPER as typifying (shaded boxes) the fish assemblages in each period, *i.e.* dry *vs*, wet in shallow, nearshore waters at Cape Keraudren and those that distinguished between the fish assemblages in each period (non-shaded box). For the pair-wise comparisons between periods, the species that distinguish the fauna of one period from that of another are indicated by the initials of that period.

	Dry	Wet
Dry	*Craterocephalus mugiloides* *Arrhamphus sclerolepis* *Sillago analis* *Sillago vittata*	
Wet	*Craterocephalus mugiloides* [W] *Strongylura strongylura* [W]	*Craterocephalus mugiloides* *Arrhamphus sclerolepis* *Strongylura strongylura* *Sillago analis*

3.3.5. Species in intertidal pools

A total of 3281 fish, representing 82 species and 38 families and weighing 15.6 kg, was collected using the ichthyocide rotenone in intertidal pools at Cape Keraudren and Port Smith (**Table 3.15**). Nineteen of the 82 species were of commercial and recreational importance and contributed 23.1% to the total catch of fish. A further five species were important to recreational fishers. The most abundant species (and their percentage contributions to the total catch) were the glassfish *Ambassis vachellii* (32.5%), the atherinids, *C. capreoli* (14.4%) and *Atherinomorus lacunosus* (7.5%), and the Moses Snapper *Lutjanus russelli* (5.2%), of which only the last is fished commercially or recreationally. The top ranked species in terms of biomass was the Estuary Rockcod *Epinephelus coioides* (19.3%), the total lengths of which ranged from 22 to 302 mm, followed by *Liza macrolepis* (13.3%) and *L. russelli* (8.3%) (**Table 3.15**). Species that were fished commercially and/or recreationally contributed 68.7% to the total weight of fish collected in intertidal pools.

Table 3.15. Rank by abundance (R), number (N), percentage contribution by number (%) and length range of each fish species caught using rotenone in intertidal pools at Port Smith and Cape Keraudren. The ranking by weight, the total weight (g) and percentage contribution by weight of each species is also given. J, occurred as juveniles, A, occurred as adults; C, commercially fished; R, recreationally fished.

		Numbers									Weight			Length	Life	
		Total			Port Smith			Cape Keraudren			Total			Range	Cycle	Fisheries
Family	Species	R	N	%	R	N	%	R	N	%	R	g	%	(mm)		
Chandidae	*Ambassis vachellii*	1	1066	32.5	3	171	10.9	1	895	52.3	6	1003.2	6.4	21 - 76	J, A	
Atherinidae	*Craterocephalus capreoli*	2	474	14.4	1	327	20.8	2	147	8.6	14	249.6	1.6	14 - 60	J, A	
Atherinidae	*Atherinomorus lacunosus*	3	247	7.5	2	247	15.7				13	251.5	1.6	29 - 84	J, A	
Lutjanidae	*Lutjanus russelli*	4	171	5.2	4	117	7.4	7	54	3.2	3	1300.9	8.3	26 - 159	J	C,R
Terapontidae	*Amniataba caudavittatus*	5	143	4.4	45	1	0.1	3	142	8.3	8	815.3	5.2	19 - 126	J, A	
Mugilidae	*Liza macrolepis*	6	125	3.8	20	10	0.6	4	115	6.7	2	2078.1	13.3	16 - 223	J, A	C,R
Gerreidae	*Gerres subfasciatus*	7	117	3.6	6	75	4.8	8	42	2.5	11	427.0	2.7	23 - 110	J, A	
Sillaginidae	*Sillago vittata*	8	100	3.0	5	100	6.4				17	165.2	1.1	21 - 106	J	C,R
Sparidae	*Acanthopagrus latus*	9	80	2.4	25	7	0.4	5	73	4.3	7	885.5	5.7	23 - 124	J, A	C,R
Serranidae	*Epinephelus coioides*	10	73	2.2	8	56	3.6	10	17	1.0	1	3007.9	19.3	22 - 302	J	C,R
Gobiidae	*Favonigobius lateralis*	11	72	2.2	7	72	4.6				44	7.7	>0.1	14 - 33	J, A	
Gerreidae	*Gerres oyena*	12	71	2.2	9	45	2.9	9	26	1.5	21	115.9	0.7	14 - 84	J, A	
Mugilidae	*Liza subviridis*	13	64	2.0				6	64	3.7	5	1044.5	6.7	41 - 198	J, A	C,R
Pomacentridae	*Abudefduf septemfasciatus*	14	44	1.3	10	39	2.5	20	5	0.3	15	197.2	1.3	14 - 116	J, A	
Platycephalidae	*Platycephalus endrachtensis*	15	36	1.1	11	35	2.2	33	1	0.1	18	164.5	1.1	12 - 153	J	R
Blenniidae	*Omobranchus germaini*	16	27	0.8	13	25	1.6	25	2	0.1	40	13.5	0.1	18 - 69	J, A	
Sillaginidae	*Sillago burrus*	17	26	0.8	12	26	1.7				35	19.4	0.1	25 - 74	J	C,R
Gobiidae	*Drombus triangularis*	18	25	0.8	16	18	1.1	16	7	0.4	41	13.3	0.1	13 - 55	J, A	
Gobiidae	*Glossogobius circumspectus*	19	24	0.7	14	23	1.5	33	1	0.1	27	42.2	0.3	31 - 75	J, A	
Gobiidae	*Acentrogobius caninus*	20	21	0.6	22	9	0.6	14	12	0.7	33	28.7	0.2	12 - 83	J, A	
Gobiidae	*Bathygobius meggetti*	21	20	0.6	15	20	1.3				29	33.2	0.2	14 - 83	J, A	
Serranidae	*Epinephelus malarbaricus*	22”	17	0.5	32	3	0.2	11	14	0.8	9	737.9	4.7	23 - 286	J	C,R
Serranidae	*Epinephelus quoyanus*	22”	17	0.5	20	10	0.6	16	7	0.4	10	442.2	2.8	37 - 172	J, A	C,R
Gobiidae	*Youngeichthys nebulosus*	24	16	0.5	37	2	0.1	11	14	0.8	26	49.9	0.3	25 - 74	J, A	
Tetraodontidae	*Arothron manilensis*	25”	15	0.5	17	15	1.0				4	1060.9	6.8	96 - 163	J, A	
Platycephalidae	*Leviprora inops*	25”	15	0.5	18	13	0.8	25	2	0.1	24	55.3	0.4	24 - 154	J	R
Mugilidae	*Valamugil buchanani*	27	13	0.4				13	13	0.8	19	161.0	1.0	53 - 156	J, A	C,R

Table 3.15. continued.

Family	Species	Numbers									Weight			Length Range (mm)	Life Cycle	Fisheries
		Total			Port Smith			Cape Keraudren			Total					
		R	N	%	R	N	%	R	N	%	R	g	%			
Mugilidae	*Valamugil perusii*	28	11	0.3	19	11	0.7				20	121.3	0.8	76 - 132	J, A	C,R
Acanthuridae	*Acanthurus grammoptilus*	29”	10	0.3	25	7	0.4	23	3	0.2	23	84.3	0.5	31 - 93	J, A	
Terapontidae	*Terapon jarbua*	29”	10	0.3				15	10	0.6	34	21.6	0.1	40 - 72	J, A	
Serranidae	*Cephalopholis boenak*	31”	9	0.3	22	9	0.6				12	377.5	2.4	34 - 235	J	C,R
Pleuronectidae	*Psammodiscus ocellatus*	31”	9	0.3	22	9	0.6				28	34.4	0.2	18 - 94	J	
Eleotridae	*Butis butis*	33”	7	0.2				16	7	0.4	31	30.9	0.2	48 - 109	J, A	
Lutjanidae	*Lutjanus argentimaculatus*	33”	7	0.2				16	7	0.4	22	94.9	0.6	48 - 114	J	C,R
Siganidae	*Siganus fuscescens*	35	6	0.2	27	6	0.4				30	31.4	0.2	60 - 77	J	
Gobiidae	*Bathygobius laddi*	36”	5	0.2	28	5	0.3				82	0.1	>0.1	9 - 11	J, A	
Mugilidae	*Mugil cephalus*	36”	5	0.2				20	5	0.3	16	170.0	1.1	138 - 156	J, A	C,R
Terapontidae	*Pelates sexlineatus*	36”	5	0.2				20	5	0.3	49	5.0	>0.1	34 - 52	J, A	
Scorpaenidae	*Paracentropogon vespa*	39”	4	0.1	29	4	0.3				54	2.9	>0.1	18 - 43	J	
Gobiidae	*Priolepis semidoliatus*	39”	4	0.1	29	4	0.3				64	0.9	>0.1	25 - 26	J, A	
Monocanthidae	*Scobinichthys granulatus*	39”	4	0.1	29	4	0.3				50	4.8	>0.1	33 - 52	J	R
Bothidae	*Engyprosopon grandisquama*	42”	3	0.1	32	3	0.2				61	1.6	>0.1	26 - 43	J	
Syngathidae	*Festucalex scalaris*	42”	3	0.1				23	3	0.2	66	0.8	>0.1	70 - 83	A	
Blenniidae	*Omobranchus ferox*	42”	3	0.1	32	3	0.2				67	0.6	>0.1	21 - 40	J, A	
Sillaginidae	*Sillago analis*	42”	3	0.1	32	3	0.2				32	29.3	0.2	83 - 136	J	C,R
Mullidae	*Upeneus tragula*	42”	3	0.1	32	3	0.2				47	6.0	>0.1	53 - 59	J	
Chaetodontidae	*Chelmon marginalis*	47”	2	0.1	37	2	0.1				48	6.0	>0.1	42 - 57	J	
Atherinidae	*Craterocephalus mugiloides*	47”	2	0.1	37	2	0.1				72	0.3	>0.1	28 - 33	J, A	
Tripterygiidae	*Enneapterygius larsoni*	47”	2	0.1	37	2	0.1				68	0.5	>0.1	27 - 28	A	
Gobiidae	*Favonigobius melanobranchus*	47”	2	0.1	37	2	0.1				75	0.2	>0.1	17 - 22	A?	
Gobiidae	*Redigobius balteatus*	47”	2	0.1	45	1	0.1	33	1	0.1	75	0.2	>0.1	12 - 16	J, A	
Gobiidae	*Asterropteryx semipunctatus*	47”	2	0.1				25	2	0.1	75	0.2	>0.1	18 - 23	A?	
Gobiidae	*Periophthalmus argentilineatus*	47”	2	0.1				25	2	0.1	52	3.3	>0.1	44 - 63	J, A	
Haemulidae	*Plectorhinchus polytaenia*	47”	2	0.1	45	1	0.1	33	1	0.1	38	15.6	0.1	65 - 88	J	
Paralichthyidae	*Pseudorhombus arsius*	47”	2	0.1	37	2	0.1				37	16.5	0.1	26 - 120	J	R
Callionymidae	*Repomucenus russelli*	47”	2	0.1	37	2	0.1				71	0.4	>0.1	20 - 35	J	

Table 3.15. continued.

Family	Species	Numbers									Weight			Length Range (mm)	Life Cycle	Fisheries
		Total			Port Smith			Cape Keraudren			Total					
		R	N	%	R	N	%	R	N	%	R	g	%			
Scatophagidae	*Scatophagus argus*	47”	2	0.1				25	2	0.1	45	7.5	>0.1	43 - 47	J	
Scatophagidae	*Selenotoca multifasciata*	47”	2	0.1				25	2	0.1	39	15.4	0.1	65 - 76	J	
Sphyraenidae	*Sphyraena fostersi*	47”	2	0.1				25	2	0.1	43	10.3	0.1	97 - 100	J	R
Engraulididae	*Stolephorus carpentariae*	47”	2	0.1	37	2	0.1				70	0.4	>0.1	31 - 32	A	
Mugilidae	*Valamugil cunnesius*	47”	2	0.1				25	2	0.1	25	51.5	0.3	91 - 163	J, A	C,R
Apogonidae	*Cheilodipterus* sp.	62”	1	<0.1	45	1	0.1				74	0.2	>0.1	25	J	
Eleotridae	*Bostrychus sinensis*	62”	1	<0.1				33	1	0.1	51	3.6	>0.1	74	A	
Callionymidae	*Calliurichthys afilum*	62”	1	<0.1	45	1	0.1				75	0.2	>0.1	32	J	
Labridae	*Choerodon cauteroma*	62”	1	<0.1	45	1	0.1				58	2.1	>0.1	48	J	C,R
Cynoglossidae	*Cynoglossus puncticeps*	62”	1	<0.1	45	1	0.1				72	0.3	>0.1	31	J	
Pegasidae	*Eurypegasus draconis*	62”	1	<0.1	45	1	0.1				79	0.1	>0.1	8	J	
Gobiidae	*Amblygobius bynoensis*	62”	1	<0.1	45	1	0.1				69	0.5	>0.1	35	A	
Gobiidae	*Istigobius decoratus*	62”	1	<0.1				33	1	0.1	56	2.8	>0.1	71	A	
Gobiidae	*Bathygobius fuscus*	62”	1	<0.1	45	1	0.1				55	2.8	>0.1	55	J	
Chaetodontidae	*Heniochus acuminatus*	62”	1	<0.1	45	1	0.1				42	11.5	0.1	73	J	
Blenniidae	*Istiblennius meleagris*	62”	1	<0.1	45	1	0.1				57	2.7	>0.1	71	A	
Gobiidae	*Istigobius nigroocellatus*	62”	1	<0.1	45	1	0.1				58	2.1	>0.1	61	J	
Lutjanidae	*Lutjanus carponotatus*	62”	1	<0.1	45	1	0.1				53	3.0	>0.1	60	J	C,R
Blenniidae	*Omobranchus lineolatus*	62”	1	<0.1	45	1	0.1				63	1.0	>0.1	43	J	
Terapontidae	*Pelates quadrilineatus*	62”	1	<0.1	45	1	0.1				46	6.6	>0.1	78	J	
Serranidae	*Plectropomus maculatus*	62”	1	<0.1	45	1	0.1				36	18.7	0.1	109	J	C,R
Pseudomugilidae	*Pseudomugil cyanodorsalis*	62”	1	<0.1				33	1	0.1	79	0.1	>0.1	25	A	
Scorpaenidae	*Pterois antennata*	62”	1	<0.1	45	1	0.1				65	0.9	>0.1	41	J	
Clupeidae	*Herklotsichthys collettei*	62”	1	<0.1	45	1	0.1				60	1.9	>0.1	61	A	
Nemipteridae	*Scaevius milii*	62”	1	<0.1	45	1	0.1				62	1.4	>0.1	43	J	
Teleost	juvenile teleost E	62”	1	<0.1	45	1	0.1				79	0.1	>0.1	23	J	
	Total fish		3281			1571			1710							
	Number of species		82			65			39							
	Total biomass (kg)		15.58			7.86			7.72							

Although the total number and total weight of fish caught at Port Smith (1571 fish and 7.86 kg) were similar to that at Cape Keraudren (1710 fish and 7.72 kg), the total number of species recorded at Port Smith (65) was far greater than at Cape Keraudren (39) (**Table 3.15**). Furthermore, only 22 of the species, *i.e.* 27%, were common to both locations. Although most of the species unique to one location were rare at that location, others, such as *A. lacunosus* and *S. vittata,* which ranked third and eighth in terms of their contribution to the total number of fish, were recorded only at Port Smith (**Table 3.15**).

3.3.6. Number of species, densities and biomass of fish in intertidal pools

ANOVA of the number of fish species caught in replicate samples obtained from intertidal pools using rotenone at Port Smith and Cape Keraudren on each sampling occasion showed that the number of species differed significantly between locations ($p<0.01$) but not among seasons (**Table 3.16**). The mean number of species at Port Smith, 16.7, was greater than at Cape Keraudren, 11.4 (**Figure 3.5a**).

Table 3.16. Mean squares and significance levels for ANOVAs of the number of species, density and biomass per unit area of fishes in intertidal pools at Port Smith and Cape Keraudren in each season. ** $p<0.01$, * $p<0.05$

	Main effects		Interactions	
Source	Location (L)	Season (S)	L x S	Residual
Degrees of freedom	1	3	3	28
Number of species	175.9 **	37.76	15.42	14.76
Density (10 m^{-1})	0.001	0.062	0.320 **	0.067
Biomass (10 m^{-1})	0.002	0.288	0.649 *	0.146

Although ANOVA showed that neither the density nor the biomass per unit area of fish in intertidal pools differed with location or season, there was a significant interaction between location and season for both density ($p<0.01$) and biomass ($p<0.05$) (**Table 3.16**). The interaction is explained by the fact that, while the mean density of fish at Port Smith precipitously declined from 205 fish 10 m^{-2} in the early dry season to 47 fish 10 m^{-2} in the late dry season and then rose sharply to a maximum of 331 fish 10 m^{-2} in the early wet season, the opposite trends essentially occurred at Cape Keraudren, with the maximum of

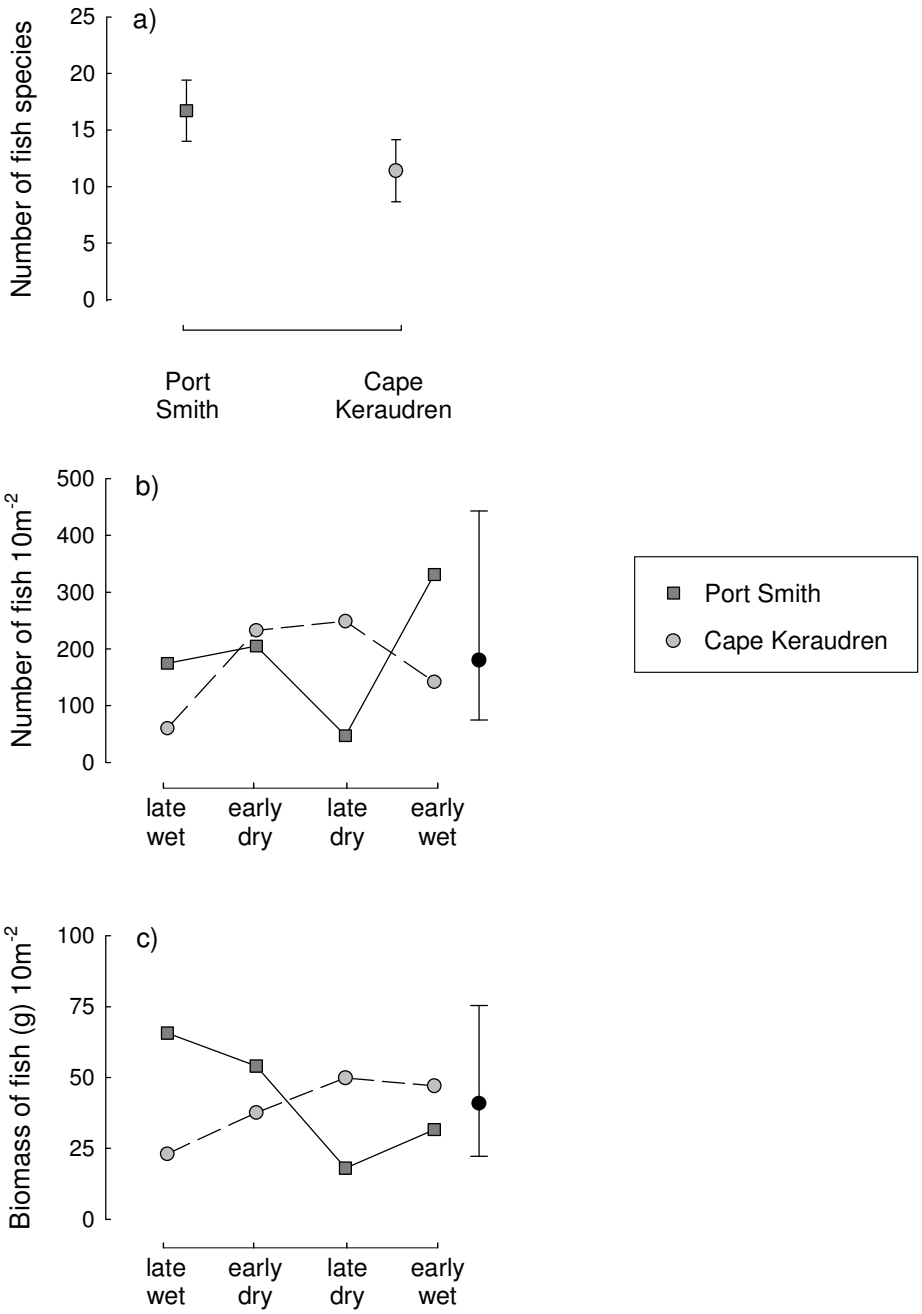

Figure 3.5. a) Mean number of fish species ± 95% CL, b) density of fish 10 m^{-2} ± 95% CL and c) biomass of fish 10 m^{-2} ± 95% CL collected with rotenone from intertidal pools at Port Smith and Cape Keraudren in each season.

248 fish 10 m^{-2} and minimum of 60 fish 10 m^{-2} being recorded in the late dry season and early wet season, respectively (**Figure 3.5b**).

The mean biomass of fish at Port Smith decreased from a maximum of *ca* 66 g $10m^{-2}$ in the late wet season to *ca* 18 g $10m^{-2}$ in the late dry season before increasing to 31.6 g $10m^{-2}$ in the early wet season (**Figure 3.5c**). In contrast, the mean biomass at Cape Keraudren increased from a minimum of *ca* 23 g $10m^{-2}$ in the late wet season to *ca* 50 g $10m^{-2}$ in the late dry season before decreasing to *ca* 47 g $10m^{-2}$ in the early wet season (**Figure 3.5c**).

3.3.7. Species compositions of fish in intertidal pools

When the mean densities of the various fish species in samples collected on the different sampling occasions from intertidal pools using rotenone were subjected to nMDS ordination, the samples from Cape Keraudren formed a group on the left of the plot that showed no overlap with the samples from Port Smith on the right of the plot (**Figure 3.6**). One-way ANOSIM confirmed that the compositions of the fish faunas in intertidal pools was very strongly influenced by location ($p<0.001$, R-statistic = 0.550). The ichthyofauna of intertidal pools at Port Smith was distinguished from that at Cape Keraudren by higher numbers of *C. capreoli* at the former location, whereas there were greater numbers of *Amniataba caudavittatus, Acanthopagrus latus* and *L. macrolepis* at Cape Keraudren (**Table 3.17**).

Figure 3.7 shows the distribution of the points for the samples obtained from intertidal pools at both Port Smith and Cape Keraudren in the early dry and late dry seasons of two years and from the early wet and late wet seasons of one year. Points for the samples from the various seasonal categories at Port Smith followed a cyclical pattern from those for late wet to early dry to late dry to early wet (**Figure 3.7a**). In contrast, no such cyclical pattern was seen in the corresponding data for Cape Keraudren (**Figure 3.7b**).

One-way ANOSIM demonstrated that there was a significant seasonal influence on the fish communities inhabiting intertidal pools at Port Smith ($p<0.01$, R-statistic = 0.307) (**Table 3.18**) and pair-wise tests revealed that the community composition of pools during the early dry season differed from the late dry season (**Table 3.19**). SIMPER revealed that

Table 3.17. Species identified by SIMPER as typifying (shaded boxes) the fish assemblages of intertidal pools at Port Smith and Cape Keraudren and those that distinguished between the fish assemblages in each location (non-shaded box). For the pair-wise comparisons between locations, the species that distinguish the fauna of one location from that of another are indicated by the initials of that location.

	Port Smith	Cape Keraudren
Port Smith	*Lutjanus russelli* *Craterocephalus capreoli* *Epinephelus coioides* *Platycephalus endrachtensis* *Atherinomorus lacunosus*	
Cape Keraudren	*Amniataba caudavittatus* CK *Acanthopagrus latus* CK *Liza macrolepis* CK *Craterocephalus capreoli* PS	*Ambassis vachellii* *Lutjanus russelli* *Amniataba caudavittatus* *Acanthopagrus latus* *Liza macrolepis*

Table 3.18. R-statistic values and significance levels for one-way ANOSIM tests for the effect of season, period (*i.e.* wet vs dry) and a severe tropical cyclone (*i.e.* immediately after cyclone *vs* pre and post cyclone conditions) on the fish fauna collected from intertidal pools at Port Smith and Cape Keraudren. ** $p<0.01$

	Port Smith	Cape Keraudren
Season	0.307 **	0.132
Period	-0.113	0.168
Cyclone	0.028	0.437 **

Table 3.19. R-statistic values and significance levels for pair-wise ANOSIM tests comparing the community composition during each of the four seasons in intertidal pools at Port Smith. * $p<0.05$

	Early dry	Late dry	Early wet
Late dry	0.372 *		
Early wet	0.200	0.127	
Late wet	0.036	0.251	0.833

Figure 3.6. Nonmetric multidimensional scaling ordination of the mean densities of the various species in samples collected using rotenone in intertidal pools at Port Smith and Cape Keraudren on each sampling occasion.

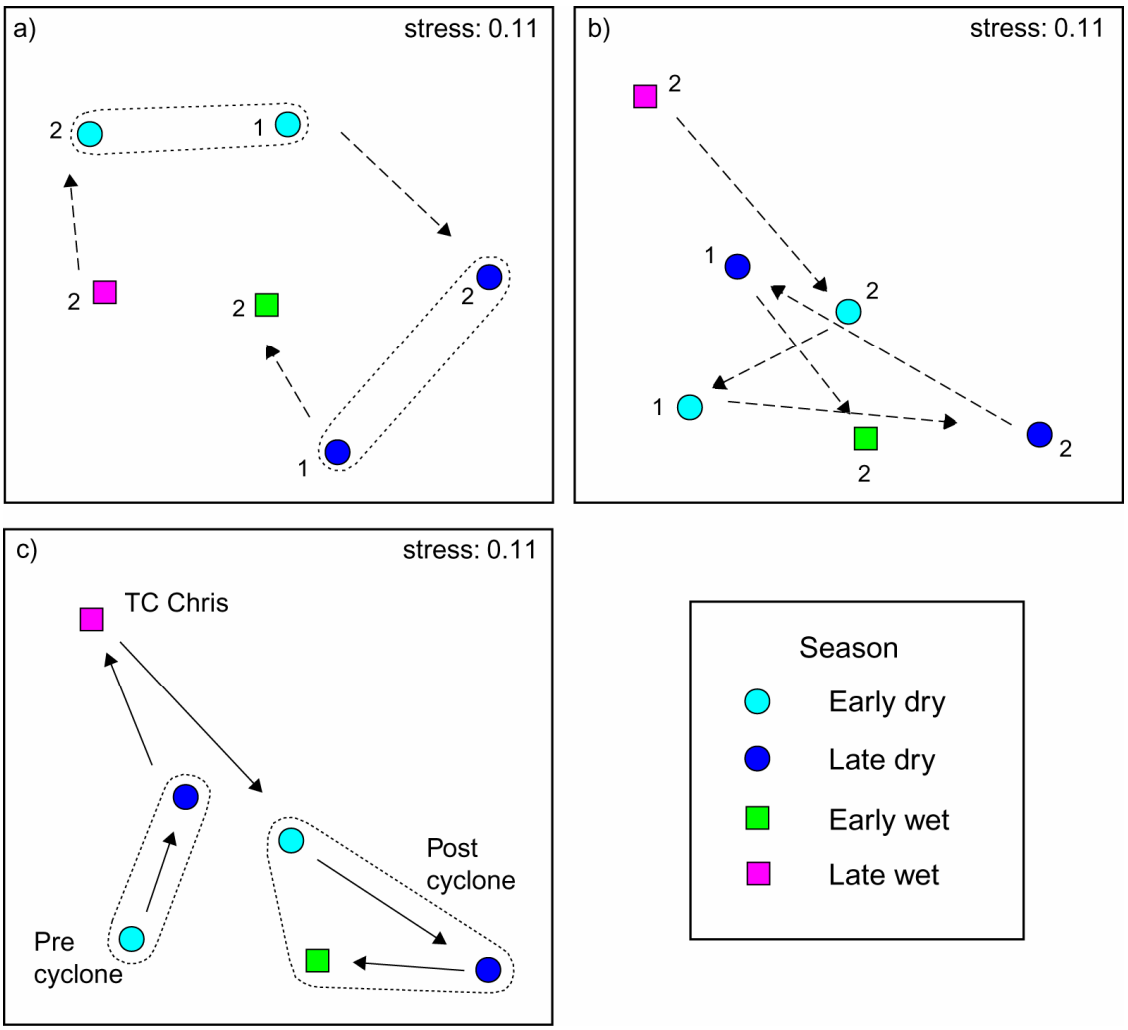

Figure 3.7. Nonmetric multidimensional scaling ordination of the mean densities of the various species in samples collected using rotenone in intertidal pools at (a) Port Smith and Cape Keraudren (b,c) on each sampling occasion. In a) and b) 1 = 2001, 2 = 2002. Dashed arrows in a) and b) represent progression by calendar month, *i.e.* Feb, May, June, Aug, Oct, Nov. Solid arrows in c) represent sequential sampling occasions, *i.e.* June, Oct, Feb, May, Aug, Nov.

this difference could be attributed to relatively greater numbers of *A. lacunosus*, *C. capreoli*, *A. vachellii* and *S. vittata* during the early dry season and *Favonigobius lateralis* and *E. coioides* during the late dry season (**Table 3.20**).

Although ANOSIM revealed that, at Cape Keraudren, neither season nor period, *i.e.* wet *vs* dry, appeared to have an overall influence on the ichthyofaunal composition of intertidal pools, the composition of intertidal pools was strongly influenced ($p<0.01$, R-statistic = 0.437) by cyclone period, *i.e.* prior to, immediately after and >3 months after Tropical Cyclone *Chris* (**Table 3.18, Figure 3.7c**). Pair-wise ANOSIM tests revealed that the composition of intertidal pools at Cape Keraudren was distinct in each cyclone period with the greatest difference ($p<0.05$, R-statistic = 0.716) occurring between the cyclone and post-cyclone periods, while the smallest difference ($p<0.05$, R-statistic = 0.304) was between the pre and post cyclone periods (**Table 3.21**). SIMPER revealed that the composition of intertidal pools immediately after Cyclone *Chris* was distinguished from pre and post cyclone samples by relatively lower numbers of *A. vachellii, A. latus,* and *L. macrolepis.* (**Table 3.22**). Higher numbers of *Ambassis vachellii* and *A. caudavittatus* and relatively lower numbers of *G. subfasciatus* distinguished post cyclone samples from pre cyclone samples (**Table 3.22**).

3.3.8. Comparison of fish faunas in nearshore, shallow waters and intertidal pools

When the mean percentage contributions of the various species in the samples obtained using the 60.5 m seine net in shallow, nearshore waters and rotenone in intertidal pools at Port Smith and Cape Keraudren on the same sampling occasions were subjected to nMDS ordination, the seine net and rotenone samples from Port Smith were located in the top half of the ordination plot and largely above the corresponding samples from Cape Keraudren (**Figure 3.8**). A both localities, the seine net samples lay to the left of the rotenone samples and were more dispersed, with MVDISP values >1.1 *vs* <0.6.

Two-way crossed ANOSIM demonstrated that the compositions of the samples differed significantly between locations ($p<0.001$, R-statistic = 0.783) and sampling methods ($p<0.001$, R-statistic = 0.688). The higher R-statistic value of 1 ($p<0.01$) at Cape Keraudren *vs* 0.632 ($p<0.001$) at Port Smith showed that the difference between the

Table 3.20. Species identified by SIMPER as typifying the fish samples collected in each season from intertidal pools at Port Smith (shaded boxes) and those that distinguished between the fish assemblages in each season (non-shaded boxes). For the pair-wise comparison between seasons, the species that distinguish the fauna of one season from that of another are indicated by the initials of that season.

	Early dry	Late dry	Early wet	Late wet
Early dry	*Lutjanus russelli* *Atherinomorus lacunosus* *Craterocephalus capreoli* *Ambassis vachellii* *Epinephelus coioides*			
Late dry	*Favonigobius lateralis* LD *Atherinomorus lacunosus* ED *Epinephelus coioides* LD *Craterocephalus capreoli* ED *Ambassis vachellii* ED *Sillago vittata* ED	*Favonigobius lateralis* *Lutjanus russelli* *Leviprora inops* *Glossogobius* sp1		
Early wet	*ns*	*ns*	*Gerres subfasciatus* *Lutjanus russelli* *Platycephalus endrachtensis* *Liza macrolepis* *Sillago vittata*	
Late wet	*ns*	*ns*	*ns*	*Craterocephalus capreoli* *Atherinomorus lacunosus* *Lutjanus russelli* *Bathygobius fuscus* *Epinephelus coioides*

Table 3.21. R-statistic values and significance levels for pair-wise ANOSIM tests comparing the community composition of intertidal pools at Cape Keraudren during each of the three cyclone periods, *i.e.* prior to, immediately after and post Cyclone *Chris* (February 2002). * $p<0.05$

	Pre cyclone	Cyclone
Cyclone	0.410 *	
Post cyclone	-0.304*	0.716 *

Table 3.22. Species identified by SIMPER as typifying (shaded boxes) the fish assemblages of intertidal pools at Cape Keraudren during each of the three cyclone periods, *i.e.* prior to, immediately after and post Cyclone *Chris* (February 2002) and those that distinguished between the fish assemblages during each period (non-shaded box). For the pair-wise comparisons between periods, the species that distinguish the fauna of one period from that of another are indicated by the prefix for that period, *i.e.* pre or post cyclone.

	Pre cyclone	Cyclone *Chris*	Post cyclone
Pre cyclone	*Ambassis vachellii* *Gerres subfasciatus* *Craterocephalus capreoli* *Acanthopagrus latus*		
Cyclone *Chris*	*Ambassis vachellii* pre *Gerres subfasciatus* pre *Acanthopagrus latus* pre *Amniataba caudavittatus* Chris *Liza macrolepis* pre	*Amniataba caudavittatus* *Craterocephalus capreoli* *Lutjanus russelli*	
Post cyclone	*Ambassis vachellii* post *Gerres subfasciatus* pre *Amniataba caudavittatus* post	*Ambassis vachellii* post *Epinephelus coioides* post *Acanthopagrus latus* post *Liza macrolepis* post	*Ambassis vachellii* *Amniataba caudavittatus* *Lutjanus russelli* *Acanthopagrus latus*

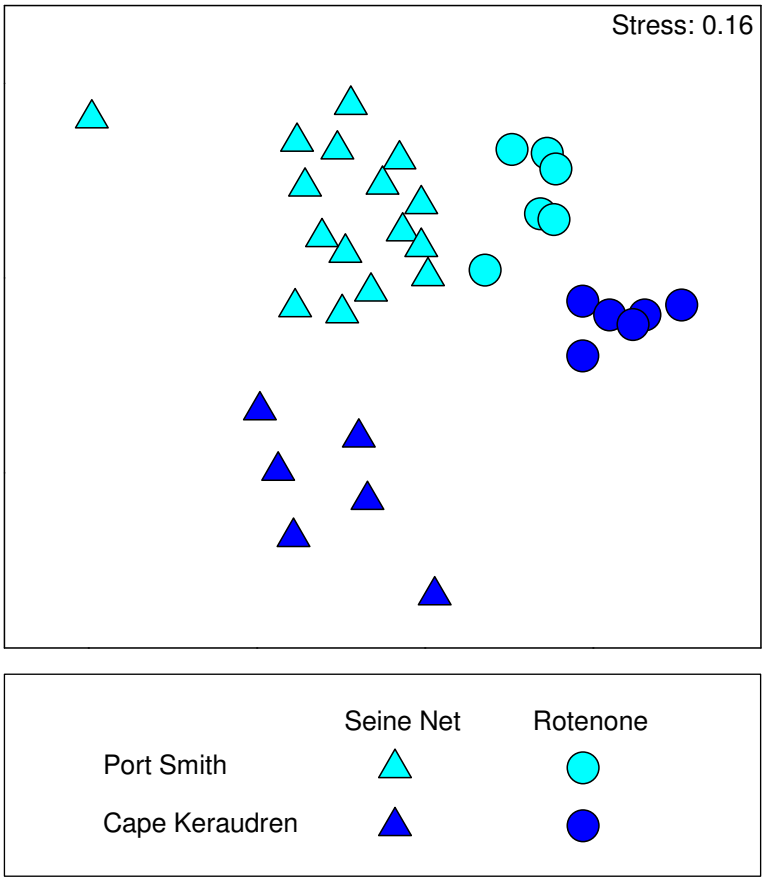

Figure 3.8. Nonmetric multidimensional scaling ordination based on the mean percentage contributions of the various species in the samples made using the 60.5 m seine net in shallow, nearshore waters and rotenone in intertidal pools at Port Smith and Cape Keraudren.

compositions of the seine and rotenone samples was greatest at Cape Keraudren. At Port Smith, SIMPER demonstrated that although *C. capreoli* and *S. vittata* were typifying species of both intertidal pools and shallow, nearshore waters, the composition of the fish fauna in these two habitats was distinguished by relatively greater numbers of a number of other species in intertidal pools including *L. russelli, P. endrachtensis, Omobranchus germaini* and *Leviprora inops* (**Table 3.24**). The difference in the community composition of intertidal pools and shallow, nearshore waters at Cape Keraudren could be attributed to relatively greater numbers of *C. mugiloides, Sillago analis* and *A. sclerolepis* in shallow, nearshore waters and *A. caudavittatus, L. russelli, E. coioides* and *A. latus* in intertidal pools (**Table 3.24**).

Table 3.24. Species identified by SIMPER as those that typified the fish assemblages in shallow, nearshore waters collected with the 60.5 m seine net and intertidal pools collected with rotenone at both Port Smith and Cape Keraudren (shaded boxes) and those that distinguished between the fish assemblages in each of those habitats (non-shaded boxes). For the pair-wise comparisons between habitats, the species that distinguish the fauna of one habitat from that of another are indicated by the initials of that habitat type.

	Port Smith		Cape Keraudren	
	Shallow, nearshore waters	Intertidal pools	Shallow, nearshore waters	Intertidal pools
Shallow, nearshore waters	*Craterocephalus capreoli* *Sillago vittata* *Atherinomorus lacunosus* *Hyporhamphus quoyi* *Gerres subfasciatus*		*Craterocephalus mugiloides* *Arrhamphus sclerolepis* *Sillago analis* *Strongylura strongylura*	
Intertidal pools	*Lutjanus russelli* IP *Platycephalus endrachtensis* IP *Omobranchus germaini* IP *Leviprora inops* IP *Drombus triangularis* IP *Epinephelus coioides* IP *Abudefduf septemfasciatus* IP	*Craterocephalus capreoli* *Lutjanus russelli* *Sillago vittata* *Platycephalus endrachtensis* *Ambassis vachellii* *Gerres oyena* *Epinephelus coioides* *Abudefduf septemfasciatus*	*Craterocephalus mugiloides* SNW *Amniataba caudavittatus* IP *Lutjanus russelli* IP *Sillago analis* SNW *Arrhamphus sclerolepis* SNW *Epinephelus coioides* IP *Acanthopagrus latus* IP *Ambassis vachellii* IP *Youngeichthys nebulosus* IP	*Ambassis vachellii* *Amniataba caudavittatus* *Liza macrolepis* *Lutjanus russelli* *Acanthopagrus latus*

3.4. Discussion

3.4.1. Ichthyofaunal compositions of nearshore shallow waters

In terms of abundance, the dominant families caught by seining in shallow, nearshore waters along the Canning coast were the Clupeidae, Atherinidae and Engraulididae, the species of which collectively accounted for >80% of the total catch. The catches were dominated by small species, as illustrated by the fact that the maximum total length of six of the seven most abundant species did not exceed 75 mm. The numerical dominance by a few, relatively small and often short-lived fish species, such as those of the above three families, is a characteristic of shallow nearshore fish faunas (*e.g.* Gibson *et al*., 1993; Clark *et al.*, 1996) and parallels the situation in similar unvegetated marine habitats in the large sub-tropical embayment Shark Bay (Black *et al*., 1990; Pember, 1999) and elsewhere in south-western Australia (Ayvazian & Hyndes, 1995; Valesini *et al*., 2004).

The ranking of the various species by abundance differed markedly among the three sampling locations. For example, the atherinid *Atherinomorus lacunosus* and the clupeid *Spratelloides delicatulus*, which were the second and fourth most abundant species at Port Smith, were never caught at neither Eighty Mile Beach nor Cape Keraudren. Similarly, the engraulid *Thryssa hamiltonii* and the clupeid *Escualosa thoracata* were almost entirely confined to the samples collected from Eighty Mile Beach, while the atherinid *Craterocephalus mugiloides* was largely restricted to the samples from Cape Keraudren. Differences in the relative abundance of the various species in shallow, nearshore waters at Port Smith, Eighty Mile Beach and Cape Keraudren account for the mean number of species, density and biomass of fish differing significantly among the three localities. Furthermore, the use of nMDS and associated ANOSIM tests revealed that the composition of the ichthyofauna inhabiting shallow, nearshore waters at Port Smith, Eighty Mile Beach and Cape Keraudren differed markedly.

As Port Smith and Cape Keraudren, the most northerly and southerly locations, respectively, are separated by more than 300km, it is not surprising that the compositions of the fish faunas in the shallow, nearshore waters of the three sampling locations were significantly different. However, the composition of the fish fauna in shallow, nearshore waters at Eighty Mile Beach was not intermediate between those at Port Smith and Cape

Keraudren, as might have been expected from their relative geographical locations. Thus, the fish faunas inhabiting shallow, nearshore waters at these three locations are presumably influenced by environmental variables not directly related to latitude, but which follow a progression from Eighty Mile Beach to Cape Keraudren to Port Smith.

The sampling locations at Eighty Mile Beach, Cape Keraudren and Port Smith are examples of the three major coastal landforms present along the Canning coast, *i.e.* an open beach, a moderately protected bay and a lagoonal-type bay protected by a narrow entrance channel, respectively. Thus, the degree of exposure to the prevailing wind and thus to wind generated waves is greatest at Eighty Mile Beach and least at Port Smith. Similarly, the very slight gradient of the beach at Eighty Mile Beach results in the surf zone being the widest at that location and narrowest at Port Smith. In addition, the width of the intertidal zone and thus the distance to permanent water is greatest at Eighty Mile Beach and least at Port Smith. The above factors result in the waters at Eighty Mile Beach being particularly turbid, while those at Port Smith are clearest. At Cape Keraudren, the clarity of the water was intermediate between that at Eighty Mile Beach and Port Smith.

Turbidity is a major influencing factor on the distribution of marine and estuarine fishes (Blaber & Blaber, 1980; Cyrus & Blaber, 1987a, b; Longhurst & Pauly, 1987). Work in tropical estuaries and nearshore waters in northern Australia has enabled species to be categorised on their ability to tolerate turbidity (Blaber *et al*., 1994). Thus, species known to have a positive association with turbid conditions include species from the Engraulididae, Ariidae, Polynemidae, Sciaenidae and some members of the Mugilidae (Blaber, 2000). It is thus relevant that the abundances of a number of species paralleled the progressive shift that occurred in turbidity between Eighty Mile Beach and Port Smith. For example, four engraulid species, four ariids, three polynemids and a single sciaenid and mugilid species were each found, either predominantly or exclusively, at Eighty Mile Beach. In contrast, those particular 13 species were not represented by a single individual at Port Smith, which had the clearest waters.

In addition to water clarity, the species compositions at Port Smith, Eighty Mile Beach and Cape Keraudren are presumably also influenced by their proximity to mangroves, which differs among the three locations. For example, the glassfish *Ambassis vachellii* was only caught in shallow, nearshore waters at Port Smith where there was an

abundance of mangroves nearby. Similarly, although atherinids were abundant at both Port Smith and Cape Keraudren, very few were caught at either of the Eighty Mile Beach sites, which are separated by >20 km from mangrove habitats. It is thus relevant that, elsewhere in sub-tropical and tropical environments, other atherinid and ambassid species are also typically associated with mangrove habitats (Rönnbäck *et al*., 1999; Ikejima *et al*., 2003; Jaafar *et al*., 2004).

The distribution of the two leiognathid species also suggests that the presence of mangroves may influence the composition of fish faunas in shallow, nearshore waters. For example, catches of *Leiognathus equulus* were restricted to the mangrove lined Port Smith, a result consistent with the finding of Blaber *et al*., (1985), that *L. equulus* was much more abundant in mangroves than in nearby unvegetated waters in the Dampier region. Similarly, Robertson & Duke (1990a) found *L. equulus* to be one of the most abundant species in mangrove-lined creeks in north-east Queensland. In contrast, the juveniles of the less abundant *Secutor insidiator* were caught at both Port Smith and Eighty Mile Beach, presumably reflecting the fact that the latter species is known to be very flexible in its choice of nursery habitats in the Gulf of Carpentaria (Staunton-Smith *et al*., 1999). The conclusion that structure of shallow water fish communities at locations along the Canning coast is influenced by the proximity of mangroves is consistent with the well documented differences in the fish assemblages of mangrove and open shore habitats in both estuarine and non-estuarine environments (e.g. Robertson & Duke, 1987; Thayer *et al*., 1987; Blaber *et al*., 1989; Sheaves, 1996; Vance *et al*., 1996).

The compositions of the fish faunas at the two sites at Port Smith and at the two sites at Eighty Mile Beach were not significantly different, whereas those at these two locations and the third location, Cape Keraudren were markedly different. At Port Smith, the lack of a significant difference between the ichthyofaunal compositions at the northern and southern sites was surprising since mangroves were located within 10 m of the southern site but more than 50 m from the northern site. The lack of differences in the composition of seine net catches at the two sites at Port Smith largely reflects the fact that the most abundant species caught with this net at both sites were schooling species, such as clupeids and engraulidids, which are pelagic zooplanktivores that move in and out of mangrove habitats (Robertson & Duke, 1990a; Ikejima *et al*., 2003).

Although there was no overall difference in the compositions of the shallow, nearshore fish faunas at the two Eighty Mile Beach sites, the densities of some of the less abundant species were greater at one or other of the sites. For example, the dasyatidids *Himantura undulata* and *Pastinachus sephen* were caught predominantly at the southern site, and thus contributed <0.1% to the total numbers of fish caught at both sites collectively and consequently had a minor effect on community structure. However, since these two rays ranked first and second in terms of biomass, their greater abundance at the southern site accounts for the large disparity in the total biomass recorded at the two sites. The unequal distribution of some species, particularly of benthic forms such as rays, at Eighty Mile Beach presumably reflect subtle differences between the two sites in environmental characteristics, *i.e.* food availability. For example, on other parts of the Eighty Mile Beach complex, the diversity and abundance of the invertebrate fauna varies considerably over relatively small distances of tens of metres due to changes in sediment characteristics such as the size, origin and depth of sediments (Wade, 2004).

3.4.2. Seasonal differences in the fish fauna of shallow, nearshore waters

The composition of the nearshore fish fauna at each of the locations underwent strong seasonal changes. This was particularly evident at Port Smith where the ichthyofaunal composition underwent progressive cyclical changes resulting from the sequential recruitment and emigration of juvenile fish into and out of shallow, nearshore waters. This progressive, seasonal change in species composition at Port Smith parallels the types of changes that have been recorded in both nearshore and offshore waters in Western Australia and elsewhere in the world (Wright, 1988; Santos & Nash, 1995; Laroche *et al*., 1997; Hyndes *et al.,* 1999).

A protracted spawning period characterises the reproductive biology of many tropical fish species and thus the recruitment period of their juveniles may be similarly extended (Conover, 1992). However, the extent and consistency of the progressive seasonal changes in community composition at Port Smith suggest that there is marked seasonality in the recruitment periods of at least a component of the ichthyofauna, presumably reflecting peaks in the spawning activity of those species. This finding is

consistent with the suggestion by Longhurst & Pauly (1987) that there is little evidence to support the assumption that the compositions of tropical fish faunas are essentially aseasonal. Moreover, Robertson & Duke (1990b) demonstrated that, while the abundance of some species in a mangrove-lined creek in Queensland varied little throughout the year, others had marked seasonal patterns in recruitment with the greatest number of species recruiting during the late dry period.

The species responsible for the progressive changes in community composition at Port Smith included *Sillago vittata, Herklotsichthys blackburni, Gerres subfasciatus* and *Psammodiscus ocellatus* during the early wet, *A. lacunosus* during the late wet, *Hyporhamphus quoyi* during the late wet and early dry and *Spratelloides delicatulus* during the early dry. Although a similar, but less pronounced, cyclical seasonal change was observed in the ichthyofaunal composition at Cape Keraudren, many of the species contributing to the change differed with *Gerres oyenya* and *H. blackburni* important during the early wet, *C. mugiloides* during the late wet and *Liza subviridis* during the early dry.

The majority of the above species were represented in seine net catches by adults as well as juveniles, reflecting the fact that these species are able to complete their life-cycle in shallow, nearshore waters and are thus residents of nearshore waters. In marked contrast, all the individuals of the sillaginid *S .vittata* collected in shallow, nearshore waters were juveniles, with lengths under that which this species typically reaches sexual maturity (Hyndes *et al*., 1996a). Thus, the above sillaginid is an example of a temporary visitor to nearshore waters, which it uses as a nursery habitat before undertaking a size-related movement to deeper waters (Hyndes *et al*., 1996b; Hyndes & Potter, 1997).

The fact that the fish fauna of shallow, nearshore waters at Port Smith appeared to undergo more pronounced seasonal cycling than at the other locations suggests that the environmental conditions at this site are particularly suitable for the recruitment of the juveniles of the species concerned. It is thus relevant that the nearshore waters sampled at Port Smith are located within a sheltered bay and thus very protected, an environmental characteristic typically associated with nearshore waters that have a high nursery value for juvenile fish (Blaber & Blaber, 1980; Lenanton, 1982; Valesini *et al*., 1997). Furthermore, the nursery function for juvenile fish provided by the shallow, nearshore waters at Port

Smith is probably enhanced by the abundance of food, and possibly shelter, offered by the surrounding mangrove habitat at this location (Robertson *et al*., 1988; Chong *et al*., 1990; Ellis & Bell, 2004; Lugendo *et al*., 2006; Verweij *et al*., 2006).

There was also a significant difference in community compositions between wet and dry periods at each of the three locations with the difference being particularly marked at Eighty Mile Beach. Examples of similar wet *vs* dry period differences in the composition of fish faunas in tropical estuaries and nearshore waters are widespread (e.g. Rooker & Dennis, 1991; Kou *et al*., 2001; Barletta *et al*., 2003; Ikejima *et al*., 2003). These ichthyofaunal differences have been attributed, at least in part, to species reacting to reduced salinities, a consequence of highly seasonal rainfall. However, the salinities of nearshore waters along the arid Canning coast remain close to that of full-strength seawater throughout the year and other environmental characteristics are presumably implicated in the change in community composition between wet and dry periods. Blaber (2000) suggests that the structure of fish communities in nearshore waters and large, open estuaries can be strongly influenced by wind-generated waves and associated increases in turbidity of such waters during the wet season. It is thus relevant that there is a marked seasonal change in the direction and strength of prevailing winds along the Canning coast, from light offshore easterlies during the dry period to moderate onshore conditions during the wet period. The fact that the wet *vs* dry difference in community structure was most pronounced at Eighty Mile Beach and least pronounced at Port Smith presumably reflects the fact that the former location is considerably more exposed to prevailing conditions than the latter location.

3.4.3. Ichthyofaunal compositions of intertidal pools

In terms of the overall abundance of fish in intertidal pools, the fish fauna was dominated by a single ambassid and atherinids, mugilids and gobiids. The Gobiidae was the richest family represented by 16 species followed by the Mugilidae, Serranidae and Blenniidae with six, five and four species, respectively. As with the fauna in shallow, nearshore waters, there was a very marked difference in the fish faunas found in intertidal pools at Port Smith and Cape Keraudren. This difference is illustrated by the fact that only 22 of

the 82 species from intertidal pools were common to both locations and the majority of the remaining species were found only at Port Smith (43 *vs* 17). While most of the species unique to Port Smith occurred in limited numbers, others such as *A. lacunosus, S. vittata* and *Favonigobius lateralis* were amongst the most abundant species at that location.

Non-metric scaling ordination and the results of ANOSIM tests demonstrated very clearly that the compositions of the fish faunas in the intertidal pools at Port Smith and Cape Keraudren differed markedly. Indeed, only *Lutjanus russelli* contributed to the suite of main typifying species of the fish faunas in the pools of both locations. The ichthyofauna of intertidal pools at Port Smith was distinguished from that at Cape Keraudren by relatively greater numbers of *C. capreoli* at the former location, whereas the opposite situation pertained with *Amniataba caudavittatus, Acanthopagrus latus* and *L. macrolepis* at Cape Keraudren.

Although the differences in the fish faunas inhabiting the intertidal pools at Port Smith and Cape Keraudren presumably reflect, in part, the fact that these locations are separated by as much as 300 km, it is highly relevant that the environmental characteristics of the pools differ considerably between the two locations. For example, in comparison with the waters at Cape Keraudren, those at Port Smith are far clearer and contain bare sand and oyster-covered rocks and little or no vegetation (see Plate 2.5). In contrast with the situation at Port Smith, the intertidal pools at Cape Keraudren are located close to mangroves and contain mangrove debris, pneumatophores and roots (see Plate 2.6) and, at high tide, their waters become confluent with those surrounding the mangrove stands.

The large areas of bare sand in the intertidal pools at Port Smith almost certainly account for the presence at this location of a greater number of sand-dwelling species, such as the sillaginids *Sillago vittata* and *Sillago burrus*, the platycephalid *Platycephalus endrachtensis* and the pleuronectid *Psammodiscus ocellatus.* Similarly, the clearer water and greater amounts of rock at Port Smith likewise accounts for the occurrence of reef-dwelling species, such as *Abudefduf septemfasciatus, Cephalopholis boenak* and *Chelmon marginalis* at this location. The marked influence that the presence of rock appears to have on the fish fauna inhabiting intertidal pools at Port Smith supports the conclusion made by Blaber *et al*. (1989) that, in tropical estuaries, the presence of rock is often accompanied

by an increased number of species in their nearshore areas. At Cape Keraudren, there were few rocky/reef species and many of the most abundant species collected at this location, such as *A. vachellii* and juveniles of *A. latus,* are typically associated with mangrove habitats (Ikejima *et al*., 2003; Platell *et al*., in press).

The only other published study of the fish faunas found in intertidal pools in north-western Australia is that of Blaber *et al*. (1985) who sampled *ca* 300 km to the south west of Cape Keraudren in the Dampier region. The overall composition of the fish fauna in intertidal pools in the Dampier region is similar to that of pools along the Canning coast, in that the Ambassidae, Gobiidae and Mugilidae are among the most abundant families (Blaber *et al*., 1985). However, the fauna at Dampier is more similar to that at Port Smith than Cape Keraudren, reflecting the presence in both locations of species of the Pomacentridae and Labridae and which, in turn, are related to occurrence of rocks /reefs at those locations. The fauna at Dampier also included some species from families typically associated with reefs, such as the Holocentridae and Muraenidae, which were not represented in the present study. Blaber *et al*., (1985) attributed the differences in the ichthyofaunal composition between Dampier and other parts of northern Australia to the presence of particularly clear water at the former location.

The structure of fish communities in intertidal pools in tropical north-western Australia differs markedly from that of the warm-temperate province of south-eastern Australia. Comprehensive sampling of intertidal pools in the latter region demonstrated that the fauna in that region is dominated by species belonging to the Gobiidae, Blenniidae, Tripterygiidae, Gobiesocidae, Clinidae and Girellidae (Lardner *et al*., 1993; Silberschneider & Booth, 2001; Griffiths, 2003a, b). The latter three families did not occur in intertidal pools in north-western Australia and the Tripterygiidae was represented by only two individuals of a single species. In this respect, the intertidal fauna of south-eastern Australia shares an affinity with that of New Zealand, which is also dominated by tripterygiid and gobiesocid species (Paulin & Roberts, 1992; Willis & Roberts, 1996).

The north-western Australian intertidal fish fauna also differs markedly from other temperate regions such as the south of South Africa where the faunas of intertidal pools are largely dominated by clinid species (e.g. Bennett & Griffiths, 1984; Beckley, 1985a, b; Bennett, 1986; Prochazka, 1996). Similarly, the Cottidae, Stichaeidae and Kyphosidae,

which characterise intertidal faunas of the north-eastern Pacific (Yoshiyama, 1981; Yoshiyama *et al*., 1986; Polivka & Chotkowski, 1998; Davis, 2000), are strikingly absent from the fish fauna of the Canning coast.

In general, there is a paucity of information regarding the fish faunas of intertidal pools in the tropical Indo-West Pacific region (Prochazka *et al*., 1999). However, there are some similarities between the composition of those in north-western Australia and those in other Indo-West Pacific locations. For example, the Gobiidae, Blenniidae, Mugilidae, Sparidae, Serranidae, Pomacentridae, Chaetodontidae and Acanthuridae are all represented in intertidal pools in north-western Australia, Taiwan (*ca* 23°N) and KwaZulu-Natal, South Africa (*ca* 30°S) (Lee, 1980a, b; Mok & Wen, 1985; Beckley, 2000). However, the KwaZulu-Natal fauna differs from the north-western Australian fauna by having a substantial temperate component and being numerically dominated by a single tripterygiid species (Beckley, 2000).

3.4.4. Seasonal differences in the fish fauna of intertidal pools

Although the mean number of species, density and biomass of fish inhabiting intertidal pools at Port Smith and Cape Keraudren were not influenced by season, the composition of the fish fauna of intertidal pools at Port Smith underwent an essentially cyclical progression over the course of a year. This pattern of change in the ichthyofaunal composition of intertidal pools, which reflects the timing and strength of recruitment of the juveniles of the various species, parallels the recruitment driven changes observed in the fauna of intertidal pools in other parts of the world (Yoshiyama, 1981; Beckley, 1985b; Willis & Roberts, 1996; Faria & Almada, 1999; Arakaki & Tokeshi, 2006).

The species most responsible for this recruitment-related change in the fish fauna of intertidal pools at Port Smith included both nearshore residents, *i.e.* species which spend their whole life cycle in nearshore waters, such as *A. vachellii, C. capreoli* and *A. lacunosus*, as well as transient species that occur only as juveniles and do not complete their life cycle in nearshore habitats, such as *Epinephelus coioides, Sillago vittata* and *Lutjanus russelli*. All of the nearshore resident species responsible for the recruitment-related “seasonality” are also found in shallow, nearshore waters and are thus not strictly

residents of intertidal pools. The fact that none of the intertidal residents that are restricted to intertidal pools, such as some of the blenniid, gobiid and pomacentrid species, were primarily responsible for the seasonal changes presumably reflects the fact that they tended to occur in small numbers and their recruitment may be limited by available habitat within intertidal pools (Gibson & Yoshiyama, 1999).

The relatively high densities of juveniles of the serranid *Epinephelus coioides* and the lutjanid *L. russelli* demonstrate that intertidal pools on the north-western Australia coast function as a nursery area for these two species which are both of significant importance to commercial fisheries offshore. The finding that all individuals of these two species, as well as of the less abundant *Epinephelus malabaricus* and *Lutjanus argentimaculatus,* caught in intertidal pools in north-western Australia were immature suggests that these species undertake a migration to deeper habitats where they mature and spawn. Such an offshore migration parallels those observed for these species in Queensland waters (Sheaves, 1995; Russell & McDougall, 2005). Similarly, elsewhere, other serranid and lutjanid species are known to use nearshore waters, including intertidal rock and mangrove pools, as nursery areas before migrating to adult habitats (Rooker, 1995; Kiso & Mahyam, 2003; Frias-Torres, 2006).

In contrast to the situation at Port Smith, the species composition of the samples from intertidal pools at Cape Keraudren did not undergo a cyclical progression. The community structure of intertidal pools was instead influenced by severe Tropical Cyclone Chris, which crossed the north-western Australia coast *ca* 25 km from the intertidal pools sampled. Thus, the composition of intertidal pools immediately after the cyclone differed from those both prior to and after the cyclone. The community immediately after the cyclone was depauparate, and was distinguished in particular by the lack of *Ambassis vachellii* and *Acanthopagrus latus*. The marked change in the fish fauna is not unexpected considering the severity of TC Chris (Category 5, winds >260 kph), which resulted in significant destruction, including the uprooting of mangroves and deposition of large amounts of debris in intertidal pools. Similar changes in community structure have been observed in temperate and sub-tropical intertidal pools following severe weather (Moring, 1996; Faria & Almada, 1999). In addition to changes related to mortality, it is also possible that the composition may change due to some species reacting to changes in

atmospheric pressure by migrating out of nearshore waters prior to the arrival of the cyclone (Heupel *et al*., 2003).

Cyclonic conditions may also result in a decline in salinity due to high rainfall and this drop in salinity has been shown to have a considerable effect on the fish faunas of estuaries (Martin *et al*., 1992). Although salinities in intertidal pools were not markedly reduced at the time of sampling (*ca* 32 ‰), they would presumably have been much lower in the hours immediately following TC Chris. It may thus be relevant that the only species to increase in abundance immediately after the cyclone was *Amniataba caudavittatus,* possibly reflecting the euryhaline nature of this terapontid (Loneragan *et al*., 1989).

3.4.5. Comparison of shallow, nearshore waters and intertidal pools

The use of percentage contribution data derived from seine netting in shallow, nearshore waters and rotenoning in intertidal pools allowed the fish communities in the two different habitats to be compared. nMDS and associated tests demonstrated that the difference in composition between the two habitats was almost as pronounced as the difference between the two locations. Such a large difference between the faunas of shallow, nearshore waters and intertidal pools, highlighted by the fact that only 25 of the 123 species caught in total were recorded in both habitats, was unexpected as these habitats are located very close to one another.

The extent of the difference was particularly marked at Cape Keraudren where the two habitats shared only eight species out of a total of 75. Each of the species found in both habitats at that location were mobile species, from the Mugilidae, Gerreidae, Atherinidae and Terapontidae, which can presumably move easily between habitats. It is also noteworthy that species from these four families are frequently associated with a range of habitats or may undertake migrations between habitats (*i.e.* Gray *et al*., 1998). Additional families that were represented in both habitats at Port Smith included the Sillaginidae, Platycephalidae, Pleuronectidae, Tetraodontidae and Ambassidae. The species from the first four families, which are typically associated with sandy substrates, presumably contribute to the intertidal pool fauna at Port Smith due to the shallow sandy margins that were characteristic of pools at that location.

Many other species were confined, or largely confined, to intertidal pools, presumably reflecting the preference of these species for structurally complex-habitats. For example, the fauna of intertidal pools at Port Smith differed from that of shallow, nearshore waters through containing a large number of species that are typically associated with rocky/reef habitats, such as the pomacentrid *A. septemfasciatus,* the serranids *C. boenak* and *Plectropomus maculatus,* the chaetodontids *Heniochus acuminatus* and *C. marginalis* and a number of blenniid species. At Cape Keraudren, the intertidal pools sampled at low tide were much closer to mangroves than the shallow, nearshore waters that were sampled during high tide. Thus, many of the species that were confined to intertidal pools at that location were mangrove associated species such as the lutjanid *Lutjanus argentimaculatus* and the scatophagids *Selenotoca multifasciata* and *Scatophagus argus* (see Chapter 4).

One of the most conspicuous differences between the faunas of the two habitats is the almost complete absence of engraulidids and clupeids in intertidal pools, families which dominated the fauna of shallow, nearshore waters at both locations. The fact that engraulidids and clupeids do not become "trapped" in intertidal pools at low tide, despite being very abundant in the surrounding waters during high tide, indicates that these species migrate to deeper waters as the tide declines. This situation contrasts with that described above for mugilids and atherinids which, while also pelagic, become "trapped" in large numbers. The confinement of mugilids and atherinids in intertidal pools but not of engraulidids and clupeids presumably reflects differences in the use, by these groups, of very shallow waters. Juvenile mugilids and atherinids, like many other small teleosts, are attracted to very shallow waters, which, while presumably minimising the threat of predation (Ellis & Bell, 2004), may result in stranding in intertidal pools. In contrast, the risk of predation for engraulidids and clupeids is minimised by forming large schools (Pitcher & Parrish, 1993) and thus, these species do not tend to be found in very shallow water.

The large differences in the compositions of the fish faunas inhabiting shallow, nearshore waters and intertidal pools at the same locations, *i.e*. at Port Smith and at Cape Keraudren, demonstrates the necessity, when undertaking research on nearshore fish

communities, to implement a sampling regime that incorporates methods appropriate for sampling the different habitats available to fish.

3.4.6. Comparison of biomass estimates

Although the biomass of fish captured in shallow, nearshore waters and in intertidal pools have been described above (3.3.2 and 3.3.5), conversion of biomass to equivalent unit per area values enables further comparison of these two habitats. The biomass collected from intertidal pools at Port Smith and Cape Keraudren stayed relatively constant at between 1.8 and 6.6 g m^{-2}, presumably reflecting the homogenous nature of the fish community recorded in this habitat and the high contribution made by species that are residents of the intertidal rather than transient species. In contrast, there was a wide range in the mean biomass collected from shallow, nearshore waters during this study. This large range may reflect, in part, the heterogenous nature of fish communities that are dominated by schooling species. However, elasmobranch species made by far the greatest contribution to the biomass of seine net samples and, as these species were encountered comparatively irregularly, are responsible for much of the variation.

The mean biomass values recorded for both shallow, nearshore waters and intertidal pools give an indication of the overall productivity of these nearshore habitats in north-western Australia. The biomass values recorded during this study for shallow, nearshore waters and intertidal pools are comparable to those recorded in the literature for other tropical habitats which typically range between 5 and 15 g m^{-2} (Blaber, 2000; **Table 3.25**). Furthermore, the high biomass recorded in shallow, nearshore waters during the late wet at Cape Keraudren of 16.3 g m^{-2} compares favourably with values for many tropical estuaries (**Table 3.25**). These values are considerably higher than those recorded for non-estuarine seagrass areas in the Northern Territory (0.5-1.8 m^{-2}) by Blaber *et al.* (1992) and presumably reflect differences in the overall productivity of these habitats (Blaber, 2000).

Table 3.25. Biomass of fish from shallow, nearshore waters and intertidal pools along the Canning coast of north-western Australia and from other sub-tropical and tropical habitats. Adapted from Blaber *et al*. (1992) and Blaber (2000).

Region	Country	Habitat	Fish biomass ($g\ m^{-2}$)
Indo-West Pacific	Australia (NW)	Nearshore waters - Port Smith	0.25 - 2.7
		Nearshore waters - Eighty Mile Beach	0.47 - 13.4
		Nearshore waters - Cape Keraudren	1.3 - 16.3
		Intertidal pools - Port Smith	1.8 - 6.6
		Intertidal pools - Cape Keraudren	2.3 - 5.0
Indo-West Pacific	Malaysia	Matang Estuary	0.25 - 3.1
	Australia	Alligator Creek	2.5 - 29.0
		Groote Eylandt - Nearshore seagrass	0.5 - 1.8.
		Embley Estuary	5.0 - 16.0
		Albatross Bay (inshore)	5.0
		Albatross Bay (offshore)	12.0 - 30.0
	Soloman Islands	Small estuaries	11.6
Tropical West Atlantic	USA, Florida	Mangrove estuaries	15.0
	Puerto Rico	Nearshore seagrass	0.65 - 3.2
	Mexico	Terminós Lagoon	0.40 - 3.4
Tropical East Pacific	Mexico	Mangrove-lined canal	7.9 - 12.5

4. Comparisons of fish faunas of unvegetated nearshore waters and mangroves.

4.1. Introduction

Mangroves are one of the most productive habitats in the nearshore waters of tropical and sub-tropical environments (Lee, 1990, 1995; Robertson *et al*., 1992; Blaber, 2000). They consequently constitute important nursery areas for several fish and crustacean species (e.g. Robertson & Duke, 1990b; Laegdsgaard & Johnson, 1995; Primavera, 1998; Nagelkerken & van der Velde, 2002) and are thus an integral component of the productivity of nearshore and offshore fisheries (Rönnbäck, 1999; Kathiresan & Bingham, 2001; Islam & Haque, 2004; Manson *et al*., 2005a, b; Sheaves, 2005; Skilleter *et al*., 2005; Mumby, 2006).

Although mangrove habitats were once distributed along *ca* 70% of coastal areas within the tropics, mangroves in certain parts of the world are becoming increasingly threatened as they are becoming cleared to provide, for example, timber and activities such as shrimp and fish culture (Nickerson, 1999; Rönnbäck, 1999; Blaber, 2000; Diop, 2003). Recent estimates suggest that more than 35% of the original area covered by mangroves has been cleared over the last two decades and consequently mangroves are now regarded as the one of the worlds most threatened ecosystems (Valiela *et al*., 2001). The fact that mangrove areas in most regions of Australia still remain relatively undamaged provides the opportunity to explore the fundamental ways in which fish species use this type of habitat and thus, in turn, ascertain the importance of their role to the fisheries of the area. Such information is critical to the sustainable management of these habitats and their species (Lee, 1999; Rönnbäck, 1999; Blaber, 2002; Halpern, 2004; Pittman *et al*., 2004; Faunce. & Serafy, 2006).

The coastline of the Canning region is the only major section of the north-western Australian coastline along which there are no major rivers and thus also estuaries. Consequently, mangroves in this arid region of the coast are restricted to tidal creeks and thus differ from the complex mangrove forests found in the northern Kimberley, where the large drainages, which receive high levels of seasonal precipitation, lead into estuaries of substantial size. In this respect, the mangrove estuaries of the Kimberley region more

closely resemble those in tropical regions elsewhere in northern Australia (*i.e.* Blaber, 1980; Blaber *et al*., 1989; Robertson & Duke, 1990a).

The mangroves in the Canning coast are further distinguished from those of the semi-arid Pilbara coast to the south in that they are located in a macrotidal environment (Eisma, 1997). Thus, for example, the spring tidal range for Broome (18°00′ S 122°13′ E) is >9.5 m, while that at Dampier (20°38′ S 116°45′ E) is typically <4.5 m. The large tidal range results in water being present in large areas of their mangrove habitats for only part of the tidal cycle and thus fish using intertidal areas for feeding or shelter must undertake substantial movements during each cycle (Rangeley & Kramer, 1995a; Gibson, 1999, 2003; Pittman & McAlpine, 2003). In contrast, large areas of mangrove habitat of tropical regions with less extreme tidal regimes, such as on the coast of Queensland, remain permanently inundated. These habitats constitute important nursery areas for a number of marine fish species (*i.e.* Sheaves, 1993, 1996, 1998).

Although mangroves are present at intervals along the Canning coast, most of the nearshore areas are unvegetated but likewise become inundated only at high tide. As studies carried out elsewhere demonstrate that the species compositions of the ichthofaunas of mangroves differ from those over nearshore unvegetated sand (*i.e.* Thayer *et al*., 1987; Chong *et al*., 1990; Nagelkerken et al., 2000a, b, 2001; Mazumder *et al*., 2005), the same situation presumably occurs along the Canning coast. However, there has been no previous study to establish whether this is the case.

The overall aim of this section of the thesis was to obtain sound quantitative data on the characteristics of the medium and large sized fish inhabiting unvegetated and mangrove areas in nearshore waters on the Canning coast of north-western Australia. For this purpose, the fish fauna was sampled using composite monofilament gill nets, which would thus provide data that complement those obtained for fish of smaller size caught by seine net in the same waters (Chapter 3). The unvegetated habitats at the three sampling locations, *i.e.* Port Smith, Eighty Mile Beach and Cape Keraudren, differed in their characteristics, and the mangroves at the first and last of those locations were also sampled. The resultant data allowed the following hypotheses to be tested. 1) The numbers of species, catch rates and compositions of the fish communities in nearshore unvegetated waters will vary among the three locations. 2) The composition of the fish fauna in

mangroves will differ from that over unvegetated sand and these differences will be maintained across regions and seasons. 3) The numbers of species and catch rates of fish in these communities will change during the year, as a result of differences in the timing and strength of recruitment of the different species. 4) Consequently the compositions of the ichthyofauna will undergo regular and consistent intra-annual cyclical changes.

4.2. Methods

4.2.1. Analysis of data for fish communities in unvegetated waters and mangroves derived from gill nets

The relationship between the mean and standard deviation for the number of fish species, the number of fish caught $3h^{-1}$ and the biomass (kg) $3h^{-1}$ for each replicate sample in unvegetated habitats at Cape Keraudren, Eighty Mile Beach and Port Smith, and the mangroves, which were present at the first and last of these locations, was examined. This demonstrated that the values for the number of fish species should be square-root transformed, while both the number and the biomass of fish caught $3h^{-1}$ should be $\log_{10}$ (n+1) transformed.

The transformed values for the number of species and catch rates for the replicate gill net samples collected over bare sand habitats at each of the three locations on each sampling occasion were subjected to two-way ANOVA to determine whether these variables differed among sites and seasons. Three-way ANOVA was employed to determine whether these three variables differed among sites and seasons and between unvegetated and mangrove habitats at Port Smith and Cape Keraudren. The data were analysed and plotted using the same procedures as described earlier for the seine net data (see Chapter 3.2.1).

The mean catch rates of each species in each gill net sample from unvegetated waters at Port Smith, Eighty Mile Beach and Cape Keraudren and in the mangroves at the first and third of these locations were analysed using nMDS ordination in the same manner as described for the seine net data (see Chapter 3.2.1). One-way and pair-wise analysis of similarities (ANOSIM) were employed to test whether the species compositions, in unvegetated habitats, at the different locations were significantly

different. Two-way crossed ANOSIM was employed to test whether the species compositions at Port Smith and Cape Keraudren, the locations where both unvegetated habitats and mangroves were sampled, differed between locations and habitats (Clarke, 1993). The R statistic values in the ANOSIM tests were used to determine which variables were most important in contributing to any significant differences.

Since the above analyses showed that the compositions of the fish faunas at the three locations and in the two habitat types at Cape Keraudren and Port Smith were significantly different (see results), nMDS ordination and ANOSIM tests were next employed to examine whether the compositions of the faunas differed significantly among seasons at each location and in each habitat type. However, since there were only two points for each "season", the replicates for each habitat type and location on each sampling occasion were used for these ordinations and associated ANOSIM tests. As with the seine net data, ANOSIM was also employed, where appropriate, to determine the degree to which the community composition was influenced by period, *i.e.* wet *vs* dry. SIMPER was again employed to determine, for each location, which species were most responsible for any dissimilarities in the species compositions of the different samples.

Since gill netting in unvegetated waters was conducted at all three locations and in effectively the same nearshore waters as was sampled with the 60.5 m seine net (see Chapter 3), the species composition of the samples collected with these two sampling methods at these three regions were compared. This comparison was based on species percentage contribution data, which were square root transformed prior to the creation of the resemblance matrix. Samples were then ordinated and 2 way crossed ANOSIM was employed to test whether the species compositions in the samples obtained using gill nets and seine nets at the different sampling regions were significantly different (Clarke 1993). SIMPER was employed to determine the species that were responsible for any differences that existed between the compositions of the samples collected with either sampling method.

4.3. Results

4.3.1. Species composition

A total of 3209 fish, representing 75 species and 36 families and weighing 2680 kg, was collected using the 60 m long gill net in unvegetated waters at Port Smith, Eighty Mile Beach and Cape Keraudren and in mangroves at Port Smith and Cape Keraudren (**Table 4.1**). Forty three of the 75 species were of commercial and recreational importance and contributed 90% to the total numbers of fish and a further nine species were important only to recreational fishers. The most abundant species (and their percentage contributions to the total catch), which were all commercially and recreationally important, were the catfish *Arius proximus* (30.8%), followed by the threadfins *Eleutheronema tetradactylum* (13.3%) and *Polydactylus macrochir* (12.5%) and the mullets *Valamugil buchanani* (9.2%) and *Liza macrolepis* (4.9%). Sixty three species contributed less than 1% and 35 of these contributed less than 0.1%.

The Green Sawfish *Pristis zijsron,* which attained lengths up to 400 cm and exceeded 33 kg in average weight, made the greatest contribution (21.4%) to the total biomass of fish (**Table 4.1**). The next ranked species in terms of biomass were *A. proximus* (13.2%), *E. tetradactylum* (12.5%) and *P. macrochir* (8.9%), while another sawfish, *Pristis microdon* (8.6%), ranked fifth. Species that are fished both commercially and recreationally accounted for 95% of the total biomass. Eighteen elasmobranch species, including the two *Pristis* species, collectively contributed 50.5% to the total weight of fish collected by gill netting. Although five of these species were amongst the top ten species in terms of biomass, they collectively contributed only 5.4% to the total number of fish and none ranked among the ten most abundant species (**Table 4.1**).

The number of species recorded in unvegetated waters and in mangroves at both Port Smith and Cape Keraudren ranged only from 34 to 39. However, the number of species was far less (24) over sand at Eighty Mile Beach where no vegetation was present in the vicinity (**Table 4.1**). Only 34 of the 69 species recorded at Port Smith and Cape Keraudren were found in both unvegetated waters and in mangrove habitats of those locations. The species that were more common in unvegetated waters than in mangroves included *E. tetradactylum, Sillago analis* and *Nematalosa come*, whereas *Plectorhinchus*

Table 4.1. Rank by abundance (R), number (N), percentage contribution by number (%) and length range of each fish species caught between December 2000 and November 2002 using the 60 m composite monofilament gill net over bare sand at Port Smith, Eighty Mile Beach and Cape Keraudren and in the mangroves at Port Smith and Cape Keraudren. The ranking by weight, total weight (kg) and percentage contribution by biomass of each species is also given. C, commercial fished; R, recreational fished.

		Number			Numbers in each region					Weight			Length Range	Life Cycle	Fisheries
		Total			Port Smith		Eighty Mile Beach	Cape Keraurdren		Total					
Family	Species	R	N	%	Sand	Mangroves	Sand	Sand	Mangroves	R	kg	%	(cm)		
Ariidae	*Arius proximus*	1	989	30.8	180	88	356	23	342	2	354.44	13.2	15 - 46	A	C,R
Polynemidae	*Eleutheronema tetradactylum*	2	426	13.3	16	4	118	262	26	3	333.98	12.5	18 - 69	J, A	C,R
Polynemidae	*Polydactylus macrochir*	3	402	12.5	3	2	341	49	7	4	239.82	8.9	19 - 117	J, A	C,R
Mugilidae	*Valamugil buchanani*	4	295	9.2	131	65		41	58	9	71.70	2.7	19 - 65	J, A	C,R
Mugilidae	*Liza macrolepis*	5	157	4.9	19	40		23	75	16	22.17	0.8	18 - 50	J, A	C,R
Carangidae	*Scomberoides commersonnianus*	6	133	4.1	8			8	117	11	51.64	1.9	21 - 52	J	C,R
Mugilidae	*Liza subviridis*	7	104	3.2	39	21		25	19	22	13.72	0.5	13 - 33	J, A	C,R
Ariidae	*Arius mastersi*	8	80	2.5			60	11	9	10	55.55	2.1	20 - 55	A	C,R
Engraulidae	*Thryssa hamiltonii*	9	72	2.2		3	54	15		33	5.27	0.2	19 - 23	J, A	
Megalopidae	*Megalops cyprinoides*	10	42	1.3	9	27			6	12	36.67	1.4	25 - 60	J, A	R
Carcharhinidae	*Carcharhinus cautus*	11	35	1.1	5	3		8	19	6	202.53	7.6	49 - 124	J, A	C,R
Sillaginidae	*Sillago analis*	12	31	1.0	11	2		12	6	37	3.95	0.1	21 - 34	J, A	C,R
Clupeidae	*Nematalosa come*	13	29	0.9	11	2	3	12	1	39	3.74	0.1	18 - 26	J, A	
Carcharhinidae	*Rhizoprionodon taylori*	14	28	0.9			28			15	24.74	0.9	36 - 69	J, A	
Carcharhinidae	*Negaprion acutidens*	15"	26	0.8	4	16	2	1	3	7	96.40	3.6	50 - 150	J	C,R
Drepanidae	*Drepane punctata*	15"	26	0.8	9	6			11	27	7.50	0.3	16 - 30	J, A	
Polynemidae	*Polydactylus multiradiatus*	15"	26	0.8			14	12		46	2.37	<0.1	18 - 22	J, A	
Chanidae	*Chanos chanos*	18"	24	0.7	21	3				21	14.32	0.5	32 - 56	A	R
Sciaenidae	*Nibea microgenys*	18"	24	0.7			19	5		42	2.60	<0.1	18 - 37	J, A	C,R
Rhinobatidae	*Rhinobatos typus*	20	23	0.7	5	6	1	7	4	14	24.78	0.9	45 - 96	J	C,R
Pristidae	*Pristis zijsron*	21"	17	0.5	1	1	1	14		1	573.65	21.4	40 - 400	J	C,R
Mugilidae	*Liza vaigiensis*	21"	17	0.5	2	6		2	7	23	13.55	0.5	29 - 51	J, A	C,R
Carangidae	*Caranx sexfasciatus*	23	16	0.5	5	1			10	30	5.76	0.2	17 - 36	J	C,R
Carcharhinidae	*Carcharhinus limbatus*	24	15	0.5	5			9	1	8	82.09	3.1	50 - 143	J	C,R

Table 4.1. continued.

		Number			Numbers in each region					Weight			Length Range	Life Cycle	Fisheries
		Total			Port Smith		Eighty Mile Beach	Cape Keraurdren		Total					
Family	Species	R	N	%	Sand	Mangroves	Sand	Sand	Mangroves	R	kg	%	(cm)		
Haemulidae	*Plectorhinchus gibbosus*	25"	11	0.3		2			9	24	10.60	0.4	26 - 56	J, A	C,R
Ariidae	*Arius argyropleuron*	25"	11	0.3	1	1	9			28	7.02	0.3	21 - 51	A	C,R
Lutjanidae	*Lutjanus argentimaculatus*	27"	10	0.3		6			4	29	5.78	0.2	25 - 41	J	C,R
Mugilidae	*Mugil cephalus*	27"	10	0.3	1		1	1	7	36	4.20	0.2	21 - 43	J, A	C,R
Carangidae	*Caranx bucculentus*	27"	10	0.3	8	2				43	2.41	<0.1	20 - 30	J	C,R
Carcharhinidae	*Carcharhinus obscurus*	30"	9	0.3				9		13	32.81	1.2	49 - 92	J	C,R
Haemulidae	*Pomadasys kaakan*	30"	9	0.3	2				7	41	2.70	0.1	25 - 36	J, A	R
Terapontidae	*Amniataba caudavittatus*	32	8	0.2	1	7				58	0.99	<0.1	14 - 25	J, A	
Carangidae	*Trachinotus blochii*	33	7	0.2	3	4				20	14.82	0.6	42 - 67	A	R
Sparidae	*Acanthopagrus latus*	34"	6	0.2	1	2		1	2	45	2.40	<0.1	21 - 32	J, A	C,R
Scatophagidae	*Selenotoca multifasciata*	34"	6	0.2		4			2	53	1.59	<0.1	20 - 25	J, A	
Clupeidae	*Herklotsichthys koningsbergeri*	34"	6	0.2				4	2	66	0.32	<0.1	16 - 18	A	
Elopidae	*Elops hawaiensis*	37	5	0.2	2	1		1	1	47	2.21	<0.1	34 - 55	J, A	R
Carcharhinidae	*Carcharhinus tilstoni*	38"	4	0.1	1		2	1		19	15.72	0.6	54 - 100	J	C,R
Sphyraenidae	*Sphyraena qenie*	38"	4	0.1		4				34	4.80	0.2	31 - 106	J, A	R
Mugilidae	*Valamugil cunnesius*	38"	4	0.1	2		2			57	1.08	<0.1	21 - 36	J, A	C,R
Dasyatididae	*Himantura undulata*	41"	3	<0.1			1	2		32	5.50	0.2	36 - 40	J, A	
Ariidae	*Arius* sp5	41"	3	<0.1			1		2	48	2.20	<0.1	33 - 53	A	C,R
Belonidae	*Strongylura strongylura*	41"	3	<0.1		2	1			62	0.50	<0.1	41 - 49	A	
Monodactylidae	*Monodactylus argenteus*	41"	3	<0.1		1			2	64	0.35	<0.1	13 - 20	J, A	
Pristidae	*Pristis microdon*	45"	2	<0.1				2		5	230.00	8.6	200 - 350	A	C,R
Carcharhinidae	*Carcharhinus amblyrhynchoides*	45"	2	<0.1			2			18	16.02	0.6	77 - 129	J	C,R
Carcharhinidae	*Carcharhinus amboinensis*	45"	2	<0.1			2			26	7.51	0.3	74 - 90	J	C,R
Latidae	*Lates calcarifer*	45"	2	<0.1	1	1				49	2.19	<0.1	45 - 47	J	C,R
Carangidae	*Caranx ignobilis*	45"	2	<0.1					2	51	1.81	<0.1	22 - 51	J	C,R
Chirocentridae	*Chirocentrus dorab*	45"	2	<0.1				2		55	1.34	<0.1	59 - 62	A	R
Belonidae	*Strongylura incisa*	45"	2	<0.1	1	1				59	0.76	<0.1	59 - 59	A	

Table 4.1. continued.

		Number			Numbers in each region					Weight					
		Total			Port Smith		Eighty Mile Beach	Cape Keraurdren		Total			Length Range	Life Cycle	Fisheries
Family	Species	R	N	%	Sand	Mangroves	Sand	Sand	Mangroves	R	kg	%	(cm)		
Belonidae	*Tylosurus gavioloides*	45"	2	<0.1	1	1				60	0.70	<0.1	61 - 63	A	
Leiognathidae	*Leiognathus equulus*	45"	2	<0.1	1				1	67	0.27	<0.1	16 - 21	A	
Rhynchobatidae	*Rhynchobatus australiae*	54"	1	<0.1			1			17	20.00	0.7	200	J	C,R
Sphyrinidae	*Eusphyra blochii*	54"	1	<0.1				1		25	10.30	0.4	130	J	C,R
Sphyrinidae	*Sphyrna lewini*	54"	1	<0.1	1					31	5.54	0.2	110	J	C,R
Sciaenidae	*Protonibea diacanthus*	54"	1	<0.1			1			35	4.36	0.2	76	J	C,R
Dasyatididae	*Pastinachhus sephen*	54"	1	<0.1				1		38	3.90	0.1	49	A	
Lobotidae	*Lobotes surinamensis*	54"	1	<0.1				1		40	2.73	0.1	51	A	C,R
Sparidae	*Acanthopagrus palmaris*	54"	1	<0.1		1				44	2.40	<0.1	30	A	R
Myliobatidae	*Aetobatus narinari*	54"	1	<0.1	1					50	2.16	<0.1	55	J	
Serranidae	*Epinephelus malabaricus*	54"	1	<0.1					1	52	1.77	<0.1	52	J	C,R
Scombridae	*Scomberomorus queenslandicus*	54"	1	<0.1	1					54	1.50	<0.1	50	J	C,R
Dasyatididae	*Taeniura lymma*	54"	1	<0.1				1		56	1.10	<0.1	30	A	
Ariidae	*Arius* sp4	54"	1	<0.1					1	61	0.61	<0.1	38	A	C,R
Latidae	*Psammoperca waigiensis*	54"	1	<0.1					1	63	0.45	<0.1	32	J	
Serranidae	*Epinephelus coioides*	54"	1	<0.1					1	65	0.33	<0.1	30	J	C,R
Rachycentridae	*Rachycentron canadus*	54"	1	<0.1	1					68	0.26	<0.1	37	J	C,R
Carangidae	*Pantolobus radiatus*	54"	1	<0.1	1					69	0.22	<0.1	26	J	
Lutjanidae	*Lutjanus russelli*	54"	1	<0.1		1				70	0.20	<0.1	22	J	C,R
Scatophagidae	*Scatophagus argus*	54"	1	<0.1		1				71	0.18	<0.1	22	A	
Mugilidae	*Rhinomugil nasutus*	54"	1	<0.1			1			72	0.12	<0.1	24	A	
Platycephalidae	*Platycephalus endrachtensis*	54"	1	<0.1	1					73	0.05	<0.1	20	J	R
Engraulidae	*Thryssa setirostris*	54"	1	<0.1				1		74	0.03	<0.1	16	A	
Eceneidae	*Remora remora*	54"	1	<0.1				1		74	0.03	<0.1	15	J	
	Number of fish		3209		516	338	1021	568	766						
	Number of species		75		39	36	24	34	34						
	Biomass (kg)		2678		288	224	508	1211	448						

gibbosus, Lutjanus argentimaculatus, Selenotoca multifasciata and *Monodactylus argenteus* were recorded in mangroves at both Cape Keraudren and Port Smith, but never over sand in those locations (**Table 4.1**). Although the samples from Eighty Mile Beach yielded the lowest number of species (24), they contained the greatest number of fish (1021), due, in particular, to a combination of large catches of the catfish *A. proximus* and *A. mastersi* and the threadfins *E. tetradactylum* and *P. macrochir* (**Table 4.1**). The contribution of commercially and recreationally important species to the total number of fish caught at each location ranged from 79.9% in the mangroves at Port Smith to 95.6% in the mangroves at Cape Keraudren.

The total weight of fish in samples collected from unvegetated waters at Cape Keraudren (1211.5 kg) was more than twice that recorded over bare sand at Eighty Mile Beach and Port Smith and in mangroves at Cape Keraudren and Port Smith (**Table 4.1**). The large biomass of fish caught over bare sand at Cape Keraudren, which contributed more than 45% to the total biomass recorded at all gill net sites, was due to the large number of elasmobranchs collected at this site, and in particular of sawfish (*P. zijsron* and *P. microdon*), which collectively weighed 772.6 kg.

4.3.2. Number of species, catch rate and biomass of fish

ANOVA showed that the number of species, number of fish caught $3h^{-1}$ and biomass of fish caught $3h^{-1}$ in unvegetated waters at Port Smith, Eighty Mile Beach and Cape Keraudren on each sampling occasion differed significantly ($p<0.001$ or <0.01) among seasons and also among locations in the case of the last two variables (**Table 4.2**). There was also a significant interaction between location and season in the case of both number of species and number of fish caught $3h^{-1}$.

The highest and lowest mean number of species in any season of 15 and 3 were recorded at Cape Keraudren during the late wet and early wet seasons, respectively (**Figure 4.1a**). In contrast, the mean seasonal number of species caught in unvegetated waters at Eighty Mile Beach remained relatively constant at *ca* 4 during the late wet, early dry and late dry seasons and then rose to 6.2 during the early wet season, while those at Port Smith declined from 6.9 during the late wet season to 4 during the early and late dry

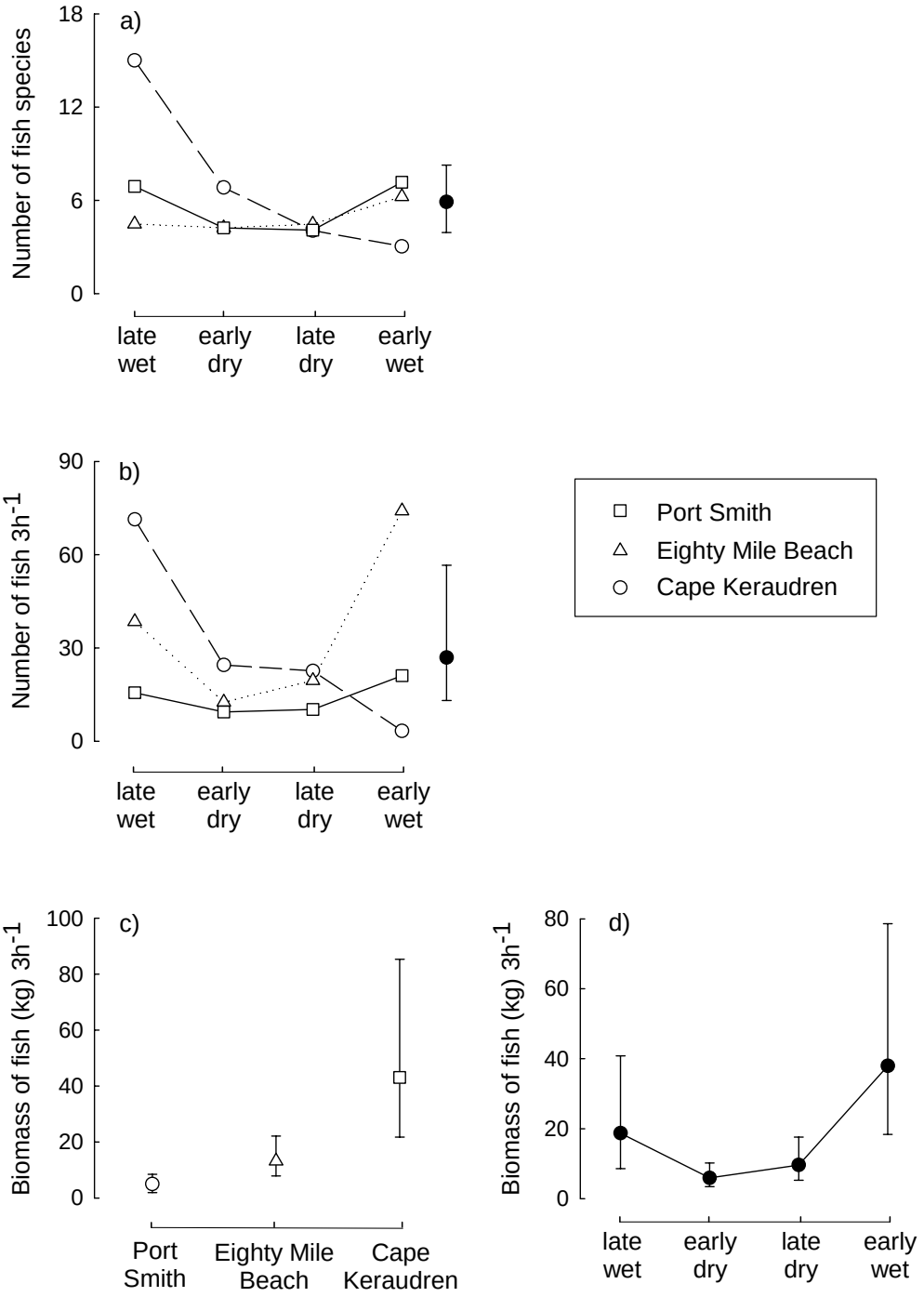

Figure 4.1. Mean values ± 95% CL for a) number of fish species, b) catch rates and c,d) biomass of fish ± 95% CL collected by the gill netting in unvegetated waters at Port Smith, Eighty Mile Beach and Cape Keraudren in each season. In this Figure and Figure 4.2 a common mean and 95% CL is shown when there are significant interactions between the main effects.

Table 4.2. Mean squares and significance levels for ANOVAs of the number of species, number of fish caught $3h^{-1}$ and biomass of fish caught $3h^{-1}$ in gill nets set in unvegetated waters at Port Smith, Eighty Mile Beach and Cape Keraudren in each season. *** $p<0.001$, ** $p<0.01$

	Main effects		Interactions	
Source	Location (L)	Season (S)	L x S	Residual
Degrees of freedom	2	3	6	63
Number of species	0.65	1.72 ***	1.29 ***	0.27
Number of fish $3h^{-1}$	0.67 **	0.38 **	0.70 ***	0.11
Biomass of fish $3h^{-1}$	4.24 ***	2.09 ***	0.03	0.34

season, before rising again to 7.1 during the early wet season (**Figure 4.1a**). The markedly different trends exhibited by the mean numbers of species at the three locations over the four seasons accounts for the strong interaction between location and season (**Table 4.2**). The trends exhibited by the catch rates of fish at the three locations over the four seasons were similar to those described for number of species. Thus, for example, the highest and lowest mean catch rates of 71.4 and 3.3 fish $3h^{-1}$ were recorded at Cape Keraudren during the late wet and early wet seasons, respectively (**Figure 4.1b**).

The mean biomass of fish caught $3h^{-1}$ was significantly greater at Cape Keraudren ($p<0.05$) than at Eighty Mile Beach, which, in turn, was significantly greater ($p<0.05$) than at Port Smith (**Figure 4.1c**). The mean biomass of fish $3h^{-1}$ recorded over bare sand declined from 18.7 kg $3h^{-1}$ during the late wet season to a minimum of 9.6 kg $3h^{-1}$ during the early dry season, before increasing to reach its maximum of 37.9 kg $3h^{-1}$ during the early wet season (**Figure 4.1d**). The mean biomass was significantly greater during the early wet season than during both the early dry ($p<0.01$) and late dry seasons ($p<0.05$). When the data for the mangrove as well as bare sand habitats at Port Smith and Cape Keraudren were analysed, ANOVA demonstrated that the number of species was significantly influenced by season and there was a significant interaction between location and season. The biomass of fish caught $3h^{-1}$ was significantly influenced by both location and season (**Table 4.3**).

The fact that these results parallel those produced when only the data for bare sand were analysed, accounts for the trends exhibited by the number of fish species and the biomass of fish caught $3h^{-1}$, using data for both habitat types at Cape Keraudren and Port

Table 4.3. Mean squares and significance levels for ANOVAs of the number of species, number of fish caught $3h^{-1}$ and biomass of fish caught $3h^{-1}$ in gill nets set over bare sand and in mangroves in nearshore, shallow waters at Port Smith and Cape Keraudren in each season. *** $p<0.001$, ** $p<0.01$.

	Main effects			Interactions				
Source	Location (L)	Season (S)	Habitat (H)	L x S	L x H	H x S	L x S x H	Residual
Degrees of freedom	1	3	1	3	1	3	3	15
Number of species	1.35	3.14 ***	0.11	3.25 ***	0.05	0.93	0.41	0.43
Number of fish $3h^{-1}$	1.58 **	0.30	0.01	0.94 ***	0.31	0.59 **	0.10	0.15
Biomass of fish $3h^{-1}$	10.27 ***	2.53 **	0.57	0.53	0.76	0.13	0.48	0.50

Smith (**Figures 4.2a,d,e**), being very similar to those exhibited when using the data for over bare sand at the three locations (**Figures 4.1a,c,d**).

However, when the number of fish caught $3h^{-1}$ in both habitat types at Cape Keraudren and Port Smith were subjected to ANOVA, location was the only main effect found to be significant and there was a significant interaction between not only location and season but also habitat and season (**Table 4.3**). The mean square was greater for the main effect than for either of the interactions. The catch rates at Cape Keraudren declined markedly and progressively from very high levels in the late wet season, *i.e*. 59.1 fish $3h^{-1}$, to 10.9 fish $3h^{-1}$ in the early wet season, whereas, those in the late wet, early dry and late dry seasons at Port Smith were similar, 10.2 to 8.6 fish $3h^{-1}$, and then rose to 28.0 in the early wet season (**Figure 4.2b**). The mean catch rates were greater over bare sand than in mangroves in each season except the early wet season (**Figure 4.2c**). Furthermore, the mean catch rates over bare sand were greatest in the late wet season and least in the early wet season, whereas those in mangroves were least in the late dry season and greatest in the early wet season (**Figure 4.2c**).

4.3.3. Ichthyofaunal compositions of gill net samples

When the mean catch rates of the various species in the different habitat types and locations on each gill net sampling occasion were subjected to nMDS ordination, the samples from over bare sand and in mangroves at Port Smith formed a widely dispersed group in the left half of the ordination plot, whereas those from over bare sand at Eighty Mile Beach formed a tight cluster in the extreme right of the plot (**Figure 4.3**). The samples from Cape Keraudren lay largely between those for Port Smith and Eighty Mile Beach. In the case of Port Smith, the samples from unvegetated waters lay mainly to the right of those from mangroves, while at Cape Keraudren those from over sand lay predominantly above those for mangroves (**Figure 4.3**).

A one-way ANOSIM, using just the data for unvegetated waters, confirmed that the compositions of the fish faunas in the three locations were highly significantly different ($p<0.001$, Global R-statistic = 0.656) and that the difference was greatest between those at Eighty Mile Beach and Port Smith ($p<0.01$, R-statistic = 0.873)

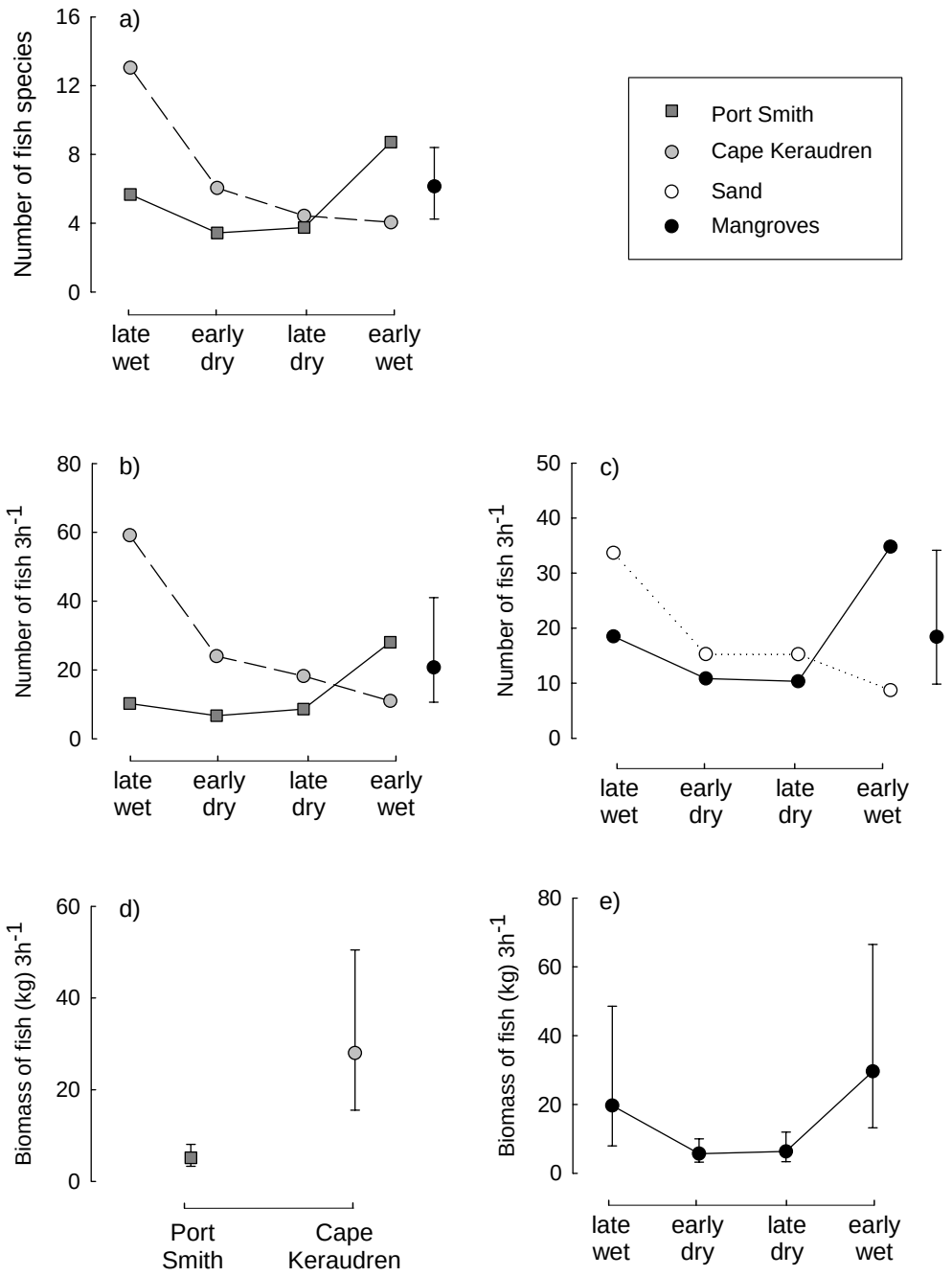

Figure 4.2. Mean values ± 95% CL for a) number of fish species, b,c) catch rates and d,e) biomass of fish ± 95% CL collected by the gill netting in unvegetated waters and in mangroves at Port Smith and Cape Keraudren in each season.

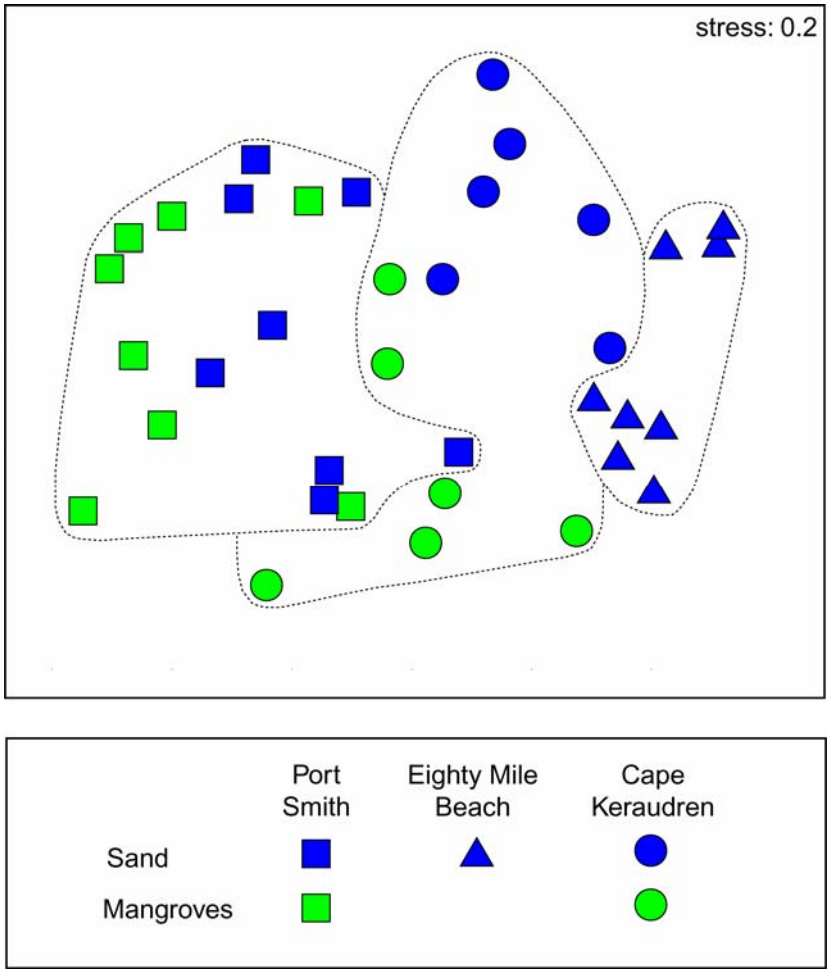

Figure 4.3. Nonmetric multidimensional scaling ordination of the mean catch rates of the various species in samples collected with the gill net in unvegetated waters at Port Smith, Eighty Mile Beach and Cape Keraudren and in mangroves at Port Smith and Cape Keraudren on each of the eight sampling occasions.

(**Table 4.4**). While SIMPER demonstrated that some species, such as *E. tetradactylum* typified the fish assemblages in unvegetated waters at all three locations, the assemblages at Port Smith, Eighty Mile Beach and Cape Keraudren were each distinguished from one another by relatively greater abundances of *V. buchanani*, *A. mastersi* and *P. zijsron*, respectively (**Table 4.5**).

Table 4.4. R-statistic values and significance levels for pair-wise ANOSIM tests comparing the community composition of samples collected with gill nets over bare sand at Port Smith, Eighty Mile Beach and Cape Keraudren. *** $p<0.001$, ** $p<0.01$

	Cape Keraudren	Eighty Mile Beach
Eighty Mile Beach	0.454 **	
Port Smith	0.514 **	0.873 ***

Two-way crossed ANOSIM, using the data for unvegetated waters and mangroves at Port Smith and Cape Keraudren, demonstrated that the compositions of the samples in these two locations were significantly different ($p<0.001$, R-statistic = 0.516), as were those between habitats ($p<0.01$, R-statistic = 0.269). Separate one-way ANOSIM tests demonstrated that this habitat difference was greater at Cape Keraudren ($p<0.05$, R-statistic = 0.337) than at Port Smith ($p<0.05$, R-statistic = 0.234). SIMPER demonstrated that, at Port Smith, relatively higher numbers of *V. buchanani, A. proximus* and *Scomberoides commersonnianus* distinguished samples from unvegetated waters, whereas *L. macrolepis* and *Megalops cyprinoides* distinguished the mangrove fish fauna at this location (**Table 4.6**). At Cape Keraudren, samples of fish collected with the gill net in unvegetated waters were distinguished from those collected in mangroves by relatively higher numbers of *P. macrochir* and *P. zijsron*, whereas mangrove samples were distinguished by relatively greater numbers of *Liza subviridis* and *Carcharhinus cautus* (**Table 4.6**).

The degree of difference between locations, *i.e.* between Port Smith and Cape Keraudren, based on the fish assemblages in mangroves was very similar to the difference observed in unvegetated waters, as demonstrated by the similar R-statistic values of 0.519 ($p<0.01$) and 0.514 ($p<0.01$), However, the species that distinguished the ichthyofaunal

Table 4.5. Species identified by SIMPER as typifying the fish samples in unvegetated waters at Port Smith, Eighty Mile Beach and Cape Keraudren (shaded boxes) and distinguished between the fish assemblages at each pair of locations (non-shaded boxes). For each pair-wise comparison between locations, the species that distinguish the fauna at one location from that at another location are indicated by the initials of that location.

	Port Smith	Eighty Mile Beach	Cape Keraudren
Port Smith	*Valamugil buchanani* *Arius proximus* *Eleutheronema tetradactylum* *Scomberoides commersonnianus*		
Eighty Mile Beach	*Polydactylus macrochir* EM *Valamugil buchanani* PS *Arius mastersi* EM *Scomberoides commersonnianus* PS *Arius proximus* EM *Eleutheronema tetradactylum* EM	*Polydactylus macrochir* *Arius proximus* *Eleutheronema tetradactylum* *Arius mastersi* *Nibea microgenys*	
Cape Keraudren	*Valamugil buchanani* PS *Polydactylus macrochir* CK *Thryssa hamiltoni* CK *Pristis zijsron* CK *Arius proximus* PS	*Polydactylus macrochir* EM *Arius mastersi* EM *Arius proximus* EM *Pristis zijsron* CK *Eleutheronema tetradactylum* EM	*Eleutheronema tetradactylum* *Pristis zijsron* *Polydactylus macrochir* *Sillago analis* *Thryssa hamiltoni*

Table 4.6. Species identified by SIMPER as typifying the fish samples in unvegetated waters and in mangroves, using data derived from gill netting, at both Port Smith and Cape Keraudren (shaded boxes) and those that distinguished between the fish assemblages in unvegetated waters and in mangroves at each location (non-shaded boxes). For the pair-wise comparisons between habitats, the species that distinguish the fauna of one habitat from that of another are indicated by the initials of that habitat type.

	Port Smith		Cape Keraudren	
	Unvegetated waters	Mangroves	Unvegetated waters	Mangroves
Unvegetated waters	*Valamugil buchanani* *Arius proximus* *Eleutheronema tetradactylum* *Scomberoides commersonnianus* *Chanos chanos*		*Eleutheronema tetradactylum* *Pristis zijsron* *Polydactylus macrochir* *Sillago analis* *Thryssa hamiltoni*	
Mangroves	*Valamugil buchanani* UW *Arius proximus* UW *Megalops cyprinoides* M *Scomberoides commersonnianus* UW *Liza macrolepis* M	*Valamugil buchanani* *Megalops cyprinoides* *Liza macrolepis* *Arius proximus*	*Polydactylus macrochir* UW *Liza subviridis* M *Pristis zijsron* UW *Carcharhinus cautus* M	*Arius proximus* *Liza subviridis* *Arius mastersi* *Eleutheronema tetradactylum* *Drepane punctata* *Carcharhinus cautus* *Liza macrolepis*

composition in mangroves at Port Smith from that in mangroves at Cape Keraudren were largely different from those that distinguished these locations in unvegetated waters. Thus, for example, SIMPER demonstrated that, while *V. buchanani* was relatively more abundant in mangroves at Port Smith than Cape Keraudren, the reverse was true for *A. mastersi, L. subviridis, L. macrolepis* and *Carcharhinus cautus.*

When the replicate catch rates of the various species in the samples collected with gill nets in unvegetated waters and in mangroves at Port Smith were subjected to nMDS ordination separately, the samples did not tend to form tight groups according to season in either habitat (**Figure 4.4a,b**). However, in both unvegetated waters and in mangroves, the points representing samples from the early wet season were largely located above and/or to the left of samples collected during the late wet season. ANOSIM illustrated that the overall composition of the fish fauna in unvegetated waters and in mangroves at Port Smith were influenced neither by season nor period (**Table 4.7**).

Table 4.7. R-statistic values and significance levels for one-way ANOSIM tests for the effect of season or period (*i.e*. wet vs dry) on the fish faunas collected in gill nets in unvegetated waters at Port Smith, Eighty Mile Beach and Cape Keraudren and from mangroves at Port Smith and Cape Keraudren. *** $p<0.001$, ** $p<0.01$, * $p<0.05$

	Port Smith		Eighty Mile Beach	Cape Keraudren	
	Sand	Mangroves	Sand	Sand	Mangroves
Season	0.044	0.078	0.542 ***	0.280 **	0.054
Period	0.024	-0.016	0.686 ***	0.280 *	0.004

Following subjection to nMDS ordination of the catch rates in the replicate gill net samples collected in unvegetated waters on each sampling occasion at Eighty Mile Beach, all but one of the samples from the early and late dry seasons lay to the right of all of those from the early and late wet seasons (**Figure 4.4c**). Furthermore, the samples from the early wet season tended to lie below those from the late wet season. ANOSIM demonstrated that the composition of the fish fauna differed significantly among seasons ($p<0.001$, Global R-statistic = 0.542) (**Table 4.7**). The greatest difference in faunal composition was

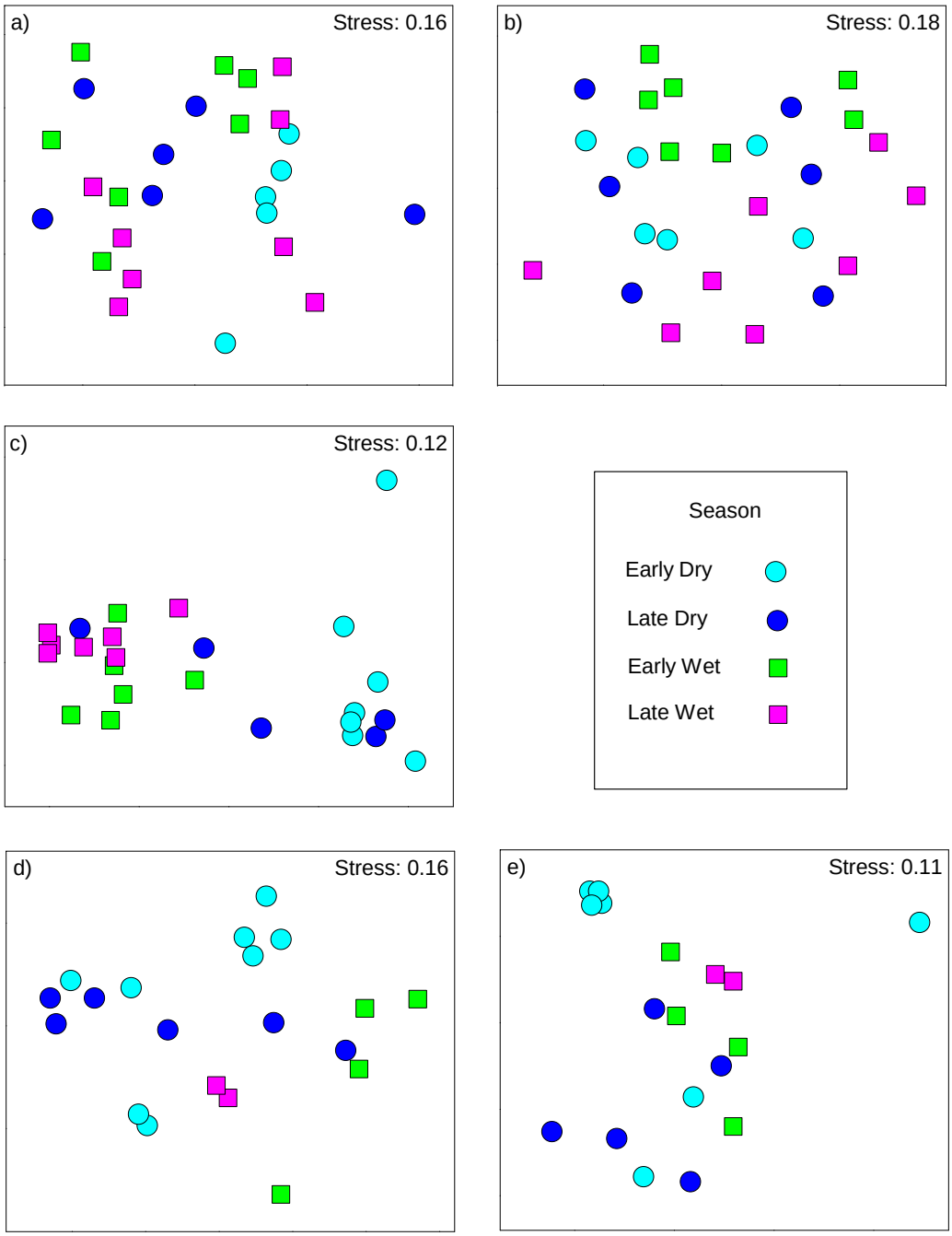

Figure 4.4. Nonmetric multidimensional scaling ordination of the catch rates of the various species in replicate samples collected with the gill net a) in unvegetated waters at Port Smith, b) in mangroves at Port Smith, c) in unvegetated waters at Eighty Mile Beach, d) in unvegetated waters at Cape Keraudren and e) in mangroves at Cape Keraudren on each sampling occasion between December 2000 and November 2002.

between the samples from the late wet season and the early dry season (p<0.001, R-statistic = 0.893) (**Table 4.8**).

Table 4.8. R-statistic values and significance levels for pair-wise ANOSIM tests comparing the community composition during each of the four seasons sampled with gill nets in unvegetated waters at Eighty Mile Beach between December 2000 and November 2002. *** p<0.001, ** p<0.01, * p<0.05

	Early dry	Late dry	Early wet
Late dry	0.162		
Early wet	0.833 **	0.502 **	
Late wet	0.893 ***	0.525 **	0.206 *

SIMPER demonstrated that the samples from the early dry were separated from those in the late wet season by relatively higher numbers of *Thryssa hamiltoni* and *E. tetradactylum* and lower numbers of *A. proximus, P. macrochir* and *A. mastersi* (**Table 4.9**). The catfishes *A. proximus* and *A. mastersi* differentiated both the early and late wet seasons from each of the dry seasons (**Table 4.9**). The only season combination at Eighty Mile Beach that was not different was that between the early and late dry seasons (**Table 4.8**). SIMPER demonstrated that both dry seasons were typified by *E. tetradactylum*, *P. macrochir* and *T. hamiltoni* (**Table 4.9**).

The tendency for the differences in community composition at Eighty Mile Beach to be greater between certain wet and dry periods is reflected in the R-statistic value for the influence of period (0.686) being greater than for season (0.542) at this location (**Table 4.7**). The species identified by SIMPER as most responsible for the considerable shift in community composition between the wet and dry periods included relatively greater numbers of *A. proximus, A. mastersi* and *P. macrochir* during the wet period and higher numbers of *E. tetradactylum* and *T. hamiltoni* during the dry period (**Table 4.10**).

When the catch rates of the various species in each sample from unvegetated waters at Cape Keraudren were subjected to ordination, the points tended to group according to season, with the samples from the early and late dry seasons typically lying above and/or to the left of those representing both the early and late wet seasons (**Figure 4.4d**). ANOSIM confirmed that the community composition in unvegetated

Table 4.9. Species identified by SIMPER as typifying the fish samples caught in each season with gill nets in unvegetated waters at Eighty Mile Beach (shaded boxes) and those that distinguished between the fish assemblages in each season (non-shaded boxes). For the pair-wise comparisons between seasons, the species that distinguish the fauna of one season from that of another are indicated by the initials of that season.

	Early dry	Late dry	Early wet	Late wet
Early dry	*Polydactylus macrochir* *Thryssa hamiltoni* *Eleutheronema tetradactylum* *Nibea microgenys*			
Late dry	*ns*	*Polydactylus macrochir* *Eleutheronema tetradactylum* *Thryssa hamiltoni*		
Early wet	*Arius proximus* EW *Arius mastersi* EW *Eleutheronema tetradactylum* EW *Polydactylus macrochir* EW	*Arius mastersi* EW *Arius proximus* EW *Thryssa hamiltoni* LD *Eleutheronema tetradactylum* EW *Polydactylus macrochir* EW	*Arius proximus* *Polydactylus macrochir* *Arius mastersi* *Eleutheronema tetradactylum*	
Late wet	*Arius proximus* LW *Thryssa hamiltoni* ED *Arius mastersi* LW *Eleutheronema tetradactylum* ED *Polydactylus macrochir* LW	*Arius proximus* LW *Eleutheronema tetradactylum* LD *Arius mastersi* LW *Polydactylus macrochir* LW	*Eleutheronema tetradactylum* EW *Arius proximus* EW	*Arius proximus* *Polydactylus macrochir* *Arius mastersi*

Table 4.10. Species identified by SIMPER as typifying (shaded boxes) the fish assemblages in each period, *i.e.* dry *vs* wet, in unvegetated waters at Eighty Mile Beach and those that distinguished between the fish assemblages in each period (non-shaded box). For the pair-wise comparisons between periods, the species that distinguish the fauna of one period from that of another are indicated by the initial of that period.

	Dry	Wet
Dry	*Polydactylus macrochir* *Eleutheronema tetradactylum* *Thryssa hamiltoni* *Nibea microgenys*	
Wet	*Arius proximus* W *Arius mastersi* W *Eleutheronema tetradactylum* D *Thryssa hamiltoni* D *Polydactylus macrochir* W	*Arius proximus* *Polydactylus macrochir* *Arius mastersi*

waters at Cape Keraudren was significantly influenced by season ($p<0.01$, Global R-statistic = 0.28) (**Table 4.7**). The difference in the composition was greatest between the late wet and late dry seasons ($p<0.05$, R-statistic = 0.563) (**Table 4.11**).

Table 4.11. R-statistic values and significance levels for pair-wise ANOSIM tests comparing the community composition during each of the four seasons sampled with gill nets in unvegetated waters at Cape Keraudren. * $p<0.05$

	Early dry	Late dry	Early wet
Late dry	0.089		
Early wet	0.463 **	0.433 *	
Late wet	-0.125	0.563 *	0.429

SIMPER demonstrated that the late wet season was distinguished from the late dry season by relatively high numbers of *Nematalosa come*, *Carcharhinus limbatus*, *Carcharhinus obscurus*, *A. proximus* and *P. macrochir* (**Table 4.12**). In addition, relatively higher numbers of *P. zijsron* and lower number of *E. tetradactylum* distinguished gill net samples during the early wet season from those of the early and late dry seasons (**Table 4.12**). ANOSIM also demonstrated that the composition of the fish

Table 4.12. Species identified by SIMPER as typifying the fish samples caught with gill nets in each season in unvegetated waters at Cape Keraudren (shaded boxes) and those that distinguished between the fish assemblages in each season (non-shaded boxes). For the pair-wise comparisons between seasons, the species that distinguish the fauna of one season from that of another are indicated by the initials of that season.

	Early dry	Late dry	Early wet	Late wet
Early dry	*Eleutheronema tetradactylum* *Liza subviridis* *Polydactylus macrochir* *Liza macrolepis* *Scomberoides commersonnianus*			
Late dry	*ns*	*Eleutheronema tetradactylum* *Pristis zijsron* *Sillago analis*		
Early wet	*Pristis zijsron* EW *Polydactylus macrochir* ED *Eleutheronema tetradactylum* ED	*Eleutheronema tetradactylum* LD *Pristis zijsron* EW	*Pristis zijsron* *Arius proximus* *Polydactylus macrochir* *Sillago analis*	
Late wet	*ns*	*Nematalosa come* LW *Carcharhinus limbatus* LW *Carcharhinus obscurus* LW *Arius proximus* LW *Polydactylus macrochir* LW	*ns*	*Polydactylus macrochir* *Nematalosa come* *Arius proximus* *Carcharhinus limbatus* *Carcharhinus obscurus*

fauna in unvegetated waters at Cape Keraudren in the wet and dry periods was significantly different ($p<0.05$, R-statistic = 0.28) (**Table 4.7**). Greater numbers of *A. proximus*, *P. macrochir* and *P. zijsron* during the wet and of *E. tetradactylum* during the dry were identified by SIMPER as most responsible for the change in community composition (**Table 4.13**).

Table 4.13. Species identified by SIMPER as typifying (shaded boxes) the fish assemblages in each period, *i.e.* dry *vs* wet, in unvegetated waters at Cape Keraudren and those that distinguished between the fish assemblages in each period (non-shaded box). For the pair-wise comparisons between periods, the species that distinguish the fauna of one period from that of another are indicated by the initials of that period.

	Dry	Wet
Dry	*Eleutheronema tetradactylum* *Polydactylus macrochir* *Sillago analis*	
Wet	*Arius proximus* W *Polydactylus macrochir* W *Eleutheronema tetradactylum* D *Pristis zijsron* W	*Polydactylus macrochir* *Pristis zijsron* *Arius proximus* *Nematalosa come*

The points representing samples collected with the gill net in mangroves at Cape Keraudren tended to be less tightly grouped according to season, with the samples from the early dry season being widely spread throughout the plot and those from the late dry season distributed towards the bottom left hand corner (**Figure 4.4e**). ANOSIM demonstrated that neither season nor period had a significant influence on the community composition in the mangroves at Cape Keraudren (**Table 4.7**).

4.3.4. Comparison of the fish faunas caught over sand using seine and gill nets

When the mean percentage contributions of the various species in the samples obtained using the 60.5 m seine net in shallow, nearshore waters and the composite gill net over unvegetated nearshore waters at all three regions, *i.e.* Port Smith, Eighty Mile Beach and Cape Keraudren, were subjected to nMDS ordination, the points representing the samples collected with gill nets were all located in the upper right hand part of the ordination plot

and were well separated from the points representing seine net samples (**Figure 4.5**). For both sampling methods, points representing samples from Cape Keraudren were located above and slightly to the left of those from Eighty Mile Beach. Seine net samples from Port Smith were located to the left of the seine samples from Cape Keraudren, whereas gill net samples from Port Smith were largely distributed above the points representing gill net samples from Cape Keraudren (**Figure 4.5**).

Two-way crossed ANOSIM demonstrated that the species compositions of the samples differed significantly among locations ($p<0.001$, R-statistic = 0.846) and between sampling methods ($p<0.001$, R-statistic = 0.899). The degree of difference between seine and gill net samples was high at both Port Smith ($p<0.01$, R-statistic = 0. 954) and Cape Keraudren ($p<0.05$, R-statistic = 0.991) and slightly less at Eighty Mile Beach ($p<0.01$, R-statistic = 0. 819).

At Port Smith, seine net samples were distinguished from gill net samples by *Craterocephalus pauciradiatus, Atherinomorus lacunosus* and *Sillago vittata* being caught with the former method, while relatively greater numbers of *V. buchanani, A. proximus* and *S. commersonnianus* were collected with the gill net (**Table 4.14**). SIMPER identified that at Eighty Mile Beach, *E. tetradactylum* and *P. macrochir* typified both seine and gill net samples. However, the former species was more common in seine net catches and the latter species in gill net samples. In addition, *Escualosa thoracata* and *Valamugil cunnesius* in seine caught samples, and *A. proximus* and *A. mastersi* in gill net samples were identified as contributing, in particular, to the differences in ichthyofaunal composition of the samples collected by these two methods at Eighty Mile Beach. At Cape Keraudren, the composition of seine samples was distinguished from that of gill net samples by *Craterocephalus mugiloides* and *Arrhamphus sclerolepis* in the former samples and *A. proximus, P. macrochir* and *P. zijsron* in the latter samples (**Table 4.14**).

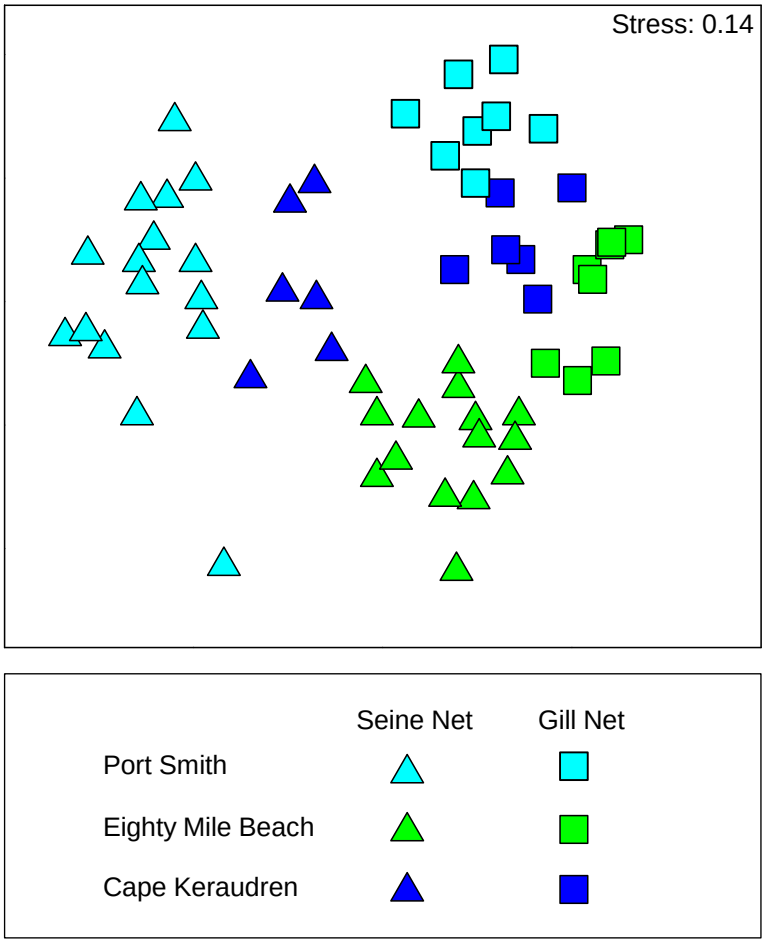

Figure 4.5. Nonmetric multidimensional scaling ordination based on the mean percentage contributions of the various species in the samples made using the 60.5 m seine net and the composite gill net in unvegetated, nearshore waters at Port Smith, Eighty Mile Beach and Cape Keraudren.

Table 4.14. Species identified by SIMPER as typifying the composition of catches made with the 60.5 m seine net and with the composite gill net in unvegetated waters at Port Smith, Eighty Mile Beach and Cape Keraudren (shaded boxes) and those that distinguished between the composition of catches made with each sampling method at each location (non-shaded boxes). For the pair-wise comparisons between sampling methods, the species that distinguish the fauna of one net type from that of the other are indicated by the initials of that sampling method.

	Port Smith		Eighty Mile Beach		Cape Keraudren	
	Seine net	Gill net	Seine net	Gill net	Seine net	Gill net
Seine net	*C. pauciradiatus* *A. lacunosus* *Sillago vittata*		*Escualosa thoracata* *Thryssa hamiltonii* *E. tetradactylum* *Valamugil cunnesius* *P. macrochir*		*C. mugiloides* *A. sclerolepis* *Sillago analis*	
Gill net	*Valamugil buchanani* GN *S. commersonnianus* GN *C. pauciradiatus* SN *Arius proximus* GN *Sillago analis* GN	*Valamugil buchanani* *Arius proximus* *S. commersonnianus* *Sillago analis*	*P. macrochir* GN *Arius mastersi* GN *Escualosa thoracata* SN *E. tetradactylum* SN *Arius proximus* GN	*P. macrochir* *Arius proximus* *Arius mastersi* *E. tetradactylum*	*C. mugiloides* SN *Arius proximus* GN *Pristis zijsron* GN *P. macrochir* GN *Sillago analis* GN *A. sclerolepis* SN	*Pristis zijsron* *P. macrochir* *E.tetradactylum* *Arius proximus* *Arius mastersi* *Sillago analis*

4.4. Discussion

4.4.1. Ichthyofaunal compositions of gill net samples

In terms of overall abundance, the fish samples collected with gill nets in unvegetated nearshore waters and mangroves in north-western Australia were dominated by the Ariidae, Polynemidae, Mugilidae, Carangidae and Carcharhinidae. These families were also amongst the richest with the Carcharhinidae, Mugilidae, Carangidae and Ariidae each represented by five or more species. Thus, the overall composition of gill net samples obtained from the nearshore waters along the Canning coast has similarities with the larger-sized fish in shallow coastal waters of other parts of the tropical Indo-West Pacific region (Blaber, 2000). However, the fish faunas of the three Canning coast locations, *i.e.* Port Smith, Eighty Mile Beach and Cape Keraudren, were notably different.

The strong influence of location on the composition of the gill net catches from nearshore waters along the Canning coast is illustrated by the fact that this variable had the most significant effect on the catch rates and biomass of fish and, interacting with season, also influenced the number of species. Furthermore, the use of nMDS and ANOSIM emphasised that the extent of the difference in the species compositions among locations was greater than among seasons and greater than the differences observed between the fish faunas in unvegetated waters and mangroves.

The composition of gill net catches obtained in unvegetated waters along the Canning coast followed a progressive change from Port Smith to Cape Keraudren to Eighty Mile Beach. Thus, the environmental variables influencing the larger ichthyofauna at these three locations do not appear directly related to latitude. The above progressive change in composition among locations parallels the trend exhibited by water clarity with the clearest water found at the protected Port Smith and the most turbid conditions found at Eighty Mile Beach (see Chapter 3.4).

As with the fish fauna collected in shallow, nearshore waters with the seine net, the types of species caught at each of the regions with gill nets were consistent with the view that turbidity has a major influence on the community composition along this coast. For example, the composition of samples from Eighty Mile Beach were distinguished from the other two locations, and particularly from Port Smith, by greater numbers of the

polynemids *Polydactylus macrochir* and *Eleutheronema tetradactylum* and the ariid catfish *Arius mastersi,* species typically associated with turbid waters (Blaber *et al*., 1995). Furthermore, some less abundant species, which are likewise typically caught in turbid waters in other coastal waters of the Indo-West Pacific, including the sharks *Carcharhinus amblyrhynchoides* and *Carcharhinus amboinensis*, the mugilid *Rhinomugil nasutus* and the sciaenid *Protonibea diacanthus,* were unique to Eighty Mile Beach. Another sciaenid *Nibea microgenys* was also caught mainly in the turbid waters of Eighty Mile Beach, presumably reflecting the preference for turbid conditions exhibited by many sciaenid species (Longhurst & Pauly, 1987; Fennessy, 1994, 2000).

In contrast to the situation at Eighty Mile Beach, *A. mastersi* and the two polynemids were caught only in low numbers at Port Smith and other species, such as the mugilid *Valamugil buchanani* and the Milkfish *Chanos chanos,* were much more abundant. It is thus relevant that, when investigating the distributions of a number of fish species in relation to various environmental parameters, Blaber *et al*. (1995) noted that the abundances of *V. buchanani* and *C. chanos* were both negatively correlated with turbidity. The association of both *V. buchanani* and *C. chanos* with waters of relatively high clarity is consistent with the fact that both of these species were also recorded in the nearshore waters at Dampier, a region likewise characterised by low turbidity (Blaber *et al*., 1985).

The biomass in gill net samples collected in unvegetated waters at Cape Keraudren was significantly greater than that obtained using the same method at Port Smith and Eighty Mile Beach reflecting the tendency of gill net samples from Cape Keraudren to contain a greater number of chondrichthyans, such as the Green Sawfish *Pristis zijsron* than the samples at the latter locations. The relatively high abundance of *P. zijsron* at Cape Keraudren and the fact that the lengths of almost all *P. zijsron* were far less than those at which this species is estimated to reach maturity, *i.e. ca* 4 m (Last & Stevens, 1994), suggests that this species may use the unvegetated nearshore waters at Cape Keraudren as a nursery habitat. Considering the endangered status of *P. zijsron* in the IUCN Red Book of Threatened Species (Compagno *et al*., 2006b), the identification of such a nursery habitat may be significant for helping ensure the long term conservation of this elasmobranch in north-western Australia.

The capture of two individuals of the Freshwater Sawfish *Pristis microdon* at Cape Keraudren is also relevent as *P. microdon* is similarly listed as endangered (Compagno *et al*., 2006a), and is believed to have suffered local extinctions within its Indo-Pacific range (Stevens *et al*., 2000; White *et al*., 2006). The fact that the larger of the two *P. microdon* caught at Cape Keraudren was a mature male suggests that this species does not use nearshore marine waters solely as a nursery area. This conclusion is consistent with the fact that the juveniles of this pristid are typically found in fresh water rivers in northern Australia (Thorburn *et al*., 2003, 2004a,b). It has been suggested that, in the Gulf of Carpentaria, *P. microdon* migrates from fresh waters to inshore marine waters to breed (Peverell, 2005) and it is thus possible that the coastal waters at Cape Keraudren may be important in supporting a breeding population of *P. microdon* along the Canning Coast of north-western Australia.

4.4.2. Ichthyofauna inhabiting unvegetated waters and mangroves

The use of the same sampling method (gill netting) to catch fish in mangroves and unvegetated waters at both Port Smith and Cape Keraudren enabled the ways in which different species use these two habitats to be investigated. Although the mean number of species, catch rate and biomass of fish in mangroves and unvegetated areas did not differ significantly, the compositions of the fish faunas caught by gill netting in these two habitats were significantly different. The habitat differences in the community compositions were greater at Cape Keraudren than at Port Smith probably due to the habitats being more separated at the former location. Despite the overall habitat difference, the suites of species that typified the faunas in the two habitat types at the above locations had little in common. For example, only *E. tetradactylum* typified unvegetated samples at both Port Smith and Cape Keraudren, while *L. macrolepis* was the only species among those typifying mangrove samples at both locations. No species distinguished the ichthyofaunal composition of either habitat from the other at both Port Smith and Cape Keraudren. The fact that different species were responsible for the habitat differences at Port Smith and Cape Keraudren indicates that other environmental factors such as turbidity assert in important influence on the fish faunas at these two locations.

At Port Smith, relatively higher numbers of the clear water mugilid *V. buchanani* and lower numbers of *Megalops cyprinoides* distinguished the species composition of unvegetated samples from those made in mangroves. The association of *M. cyprinoides* with mangrove habitats possibly reflects the fact that this species typically preys upon small prawns and fish, including ambassids (Coates, 1987), which occur in high densities in and around mangroves. In contrast, the compositions of unvegetated waters and mangroves at Cape Keraudren were distinguished by *P. macrochir* and *P. zijsron* in the former habitat and *L. subviridis* and the Nervous Shark *Carcharhinus cautus* in the latter habitat. The association of *P. macrochir* with unvegetated waters at Cape Keraudren presumably reflects the preference of this species for the more turbid conditions found over sand at that location, whereas the preference of unvegetated waters by *P. zijsron* presumably reflects the fact that this species is benthic. The use of mangroves by both the juveniles and adults of *C. cautus* demonstrates that this species completes its life cycle in nearshore waters and parallels the situation recorded for this species by White *et al*. (2002) in Shark Bay, approximately 1000 km to the south of Cape Keraudren.

The Lemon Shark *Negaprion acutidens*, like *C. cautus*, was far more abundant in mangroves than in unvegetated waters. However, in contrast to the situation for *C. cautus*, only the juveniles of the larger growing *N. acutidens* were collected in nearshore waters, suggesting that this elasmobranch uses mangroves as a nursery habitat. Such a situation parallels the use of mangrove habitats as a nursery by the closely-related *Negaprion brevirostris* in the Atlantic (Freitas *et al*., 2006). Freitas *et al*. (2006) propose that mangrove habitats offer juvenile sharks a refuge from predation by larger shark species. In addition, the results of White *et al*. (2004) suggest that the use of nearshore mangrove habitats in Shark Bay by both *C. cautus* and *N. acutidens* provides these species with diverse and abundant feeding opportunities, a conclusion consistent with dietary studies of these species conducted elsewhere in Australia (Salini *et al*., 1992).

In addition to the species described above, other less abundant species typically occurred in only one habitat. Thus, for example, the haemulid *Plectorhinchus gibbosus*, the lutjanid *Lutjanus argentimaculatus*, the scatophagids *Selenotoca multifasciata* and *Scatophagus argus*, the monodactylid *Monodactylus argenteus*, the serranids *Epinephelus*

coioides and *Epinephelus malabaricus* and the sparids *Acanthopagrus latus* and *Acanthopagrus palmaris* were all predominantly or exclusively recorded in mangroves.

Although a number of workers have documented differences in the fish faunas inhabiting mangroves and other habitats including unvegetated waters (*i.e.* Sheaves, 1992, 1996, 1998; Nagelkerken *et al*., 2000a; Nagelkerken & van der Velde, 2002), the majority of these studies have concentrated on sub-tidal waters. The very large tides that characterise the Canning coast mean that both the mangroves and unvegetated habitats sampled during this study are well separated from permanent water and the fish species using these habitats must make long tidal migrations to do so. Thus, despite the availability of mangrove habitats to fish along this coast being temporary, the benefits that fish gain by using this habitat, either in terms of increased food availability or refuge from predation, are still considerable. The consistent migration by fish into habitats that are only available temporarily suggests that such a habitat is of significant importance to the species involved (Rangeley & Kramer 1995b; Dorenbosch *et al.*, 2004).

4.4.3. Seasonal differences in the fish fauna of unvegetated waters and mangroves

The number of species caught with gill nets and the catch rate of fish in terms of both numbers and biomass in nearshore waters differed significantly between seasons with the highest values typically being recorded during the early and late wet seasons. Wet season peaks in the species richness and abundance of fish along the Canning coast parallels the situation observed for other nearshore marine and estuarine faunas in the tropics and presumably reflects both an influx of recruiting juveniles of certain species as well as the use, during the wet season, of nearshore waters by others species which benefit from the abundant food present in such areas at that time (*i.e*. Louis *et al*., 1995; Robertson & Duke, 1990a; Stoner, 1986; Flores-Verdugo *et al*., 1990; Godínez-Domínguez *et al*., 2000).

The seasonal differences in the diversity and abundance of fish caught with gill nets was reflected in marked seasonal changes in the community composition of the ichthyofauna in unvegetated waters at Eighty Mile Beach and Cape Keraudren. These changes were particularly pronounced at Eighty Mile Beach, where the composition of the

fish fauna progressed in an almost cyclical fashion caused by the varying contributions of the different species over the course of the year. The species responsible included the ariid catfishes *A. proximus* and *A. mastersi*, the polynemids *E. tetradactylum* and *P. macrochir* and the engraulidid *T. hamiltonii.* Although *E. tetradactylum*, *P. macrochir* and *A. proximus* were also responsible for much of the seasonal differences in the composition of gill net catches at Cape Keraudren, certain elasmobranch species also contributed at the latter location with the juveniles of the endangered *P. zijsron* particularly abundant during the early wet season.

The extent of the seasonal difference in the species compositions of gill net catches obtained in unvegetated waters at Eighty Mile Beach and Cape Keraudren was greatest between the two wet and the two dry seasons. This was particularly the case at Eighty Mile Beach where the influence of period, *i.e.* wet *vs* dry, was greater than the influence of season, a fact emphasised by the wide separation of the 'wet' and 'dry' samples on the ordination plot for that location. The faunal differences between these periods were mainly attributable to the relatively far greater numbers of *P. macrochir* and the catfishes *A. proximus* and *A. mastersi* during the wet period and of *T. hamiltonii* and *E. tetradactylum* during the dry period. Indeed, the two catfish species were largely caught in gill nets only during the wet period, when they were present in relatively very large numbers. This point is illustrated by the fact that the numbers of *A. proximus* caught during the wet period were over 20 times greater than that obtained during the dry period. Since many of the catfish caught during the wet period were mature, this increase in numbers presumably reflects a movement to nearshore, shallow areas where catfish are known to form spawning aggregations (Kailola *et al.,* 1993). Conversely, the absence of very small individuals of the *Arius* species in the samples obtained from nearshore waters with either gill nets or the seine net (Chapter 3) is presumably attributable to the fact that the oral-brooding adults of these species move offshore and deposit their eggs in deeper water (Blaber, 2000).

The greater biomass recorded for fish in gill net catches during the wet period of the year was due not only to greater catches of catfish but also to an increased number of elasmobranchs. The increased number of elasmobranchs during the wet period, when there are strong onshore winds, parallels the findings of Blaber *et al*. (1985) in the Gulf of

Carpentaria and presumably reflects a preference of many sharks for the turbid waters found inshore at this time. In addition, the presence of large numbers of elasmobanchs in nearshore waters during the wet period may reflect the higher water temperatures during that time of the year (Merson & Pratt, 2001; Hopkins & Cech, 2003; Hunter *et al*., 2005).

Since many of the elasmobranch species which contributed to wet season catches were recorded only as juveniles, e.g. *Negaprion acutidens*, *Pristis zijsron, Carcharhinus obscurus*, *Carcharhinus tilstoni*, *Carcharhinus amblyrhynchoides*, *Carcharhinus amboinensis*, *Eusphyra blochii* and *Sphyrna lewini*, these waters presumably perform a nursery function for these species during the wet period. The use of nearshore waters in north-western Australia as a nursery area by these species parallels the situation documented for other elasmobranchs, including carcharhinid and sphyrinid sharks, elsewhere (Castro, 1993; Simpfendorfer & Milward, 1993; Duncan & Holland, 2006; Yokota & Lessa, 2006). Although many juvenile elasmobranchs presumably make excursions into nearshore waters to forage, many authors stress the role of this shallow water habitat as an important refuge from predation by large sharks (Morrissey & Gruber, 1993; Heupel & Hueter, 2002; Heupel & Simpfendorfer, 2002; Duncan & Holland, 2006).

4.4.4. Comparison of the compositions of gill net samples and seine net samples

The use of percentage contribution data derived from gill netting and seine netting in the same unvegetated nearshore waters at Port Smith, Eighty Mile Beach and Cape Keraudren allowed the species composition of the samples caught with the two methods to be compared. nMDS and associated tests demonstrated that the species compositions in catches using the two sampling methods differed markedly and that this difference was of a similar magnitude to the overall differences in the ichthyofaunas at locations along the Canning coast. The large difference between the compositions of the samples collected with the seine and gill nets in nearshore unvegetated waters reflects the relatively small proportion of species that were caught by both sampling methods. For example, only 35 of the 120 species recorded in total by seining and gill netting in nearshore unvegetated waters were caught using both sampling methods.

The marked difference was due mainly to the tendency of seine nets to catch large numbers of very small fish, such as *Craterocephalis capreoli*, *Craterocephalis mugiliodies* and *Escualosa thoracata*, which did not reach lengths >78 mm and were thus never retained by the much larger mesh of the gill net. As seine net catches were dominated by small, relatively short-lived fishes, only two of the ten most abundant species caught by seine net, *i.e. T. hamiltonii and Leiognathus equulus,* were recorded in gill nets samples. In contrast, nine of the ten most abundant species recorded in gill net catches were also caught with the seine net. This demonstrates that, in addition to small species such as atherinids, the composition of seine net catches also has a component comprising the juveniles of larger sized nearshore species including mugililids and polynemids.

The species compositions of seine and gill net samples were most different at Port Smith and most similar at Eighty Mile Beach. The particularly marked difference at Port Smith presumably reflects the fact that many small species, not caught with gill nets, were particularly abundant at that location. Differences in the timing of the recruitment of the 0+ cohorts of these species resulted in the species composition of seine net samples undergoing pronounced seasonal cycling at Port Smith (Chapter 3). In contrast, the species composition of gill net samples at that location failed to show a consistent seasonal change, due presumably to the fact that gill nets catch few species that have been recently recruited into nearshore waters.

Differences in the composition of samples obtained by the two methods were less pronounced at Eighty Mile Beach, due to some of the most abundant species at this location being caught by both sampling methods, including, in particular, *T. hamiltonii, Polydactylus macrochir* and *Eleutheronema tetradactylum.* The fact that *T. hamiltonii* characterised the wet period in seine net catches and the dry period in gill net samples demonstrates that the two sampling methods largely target different life cycle categories of this resident of nearshore waters. For example, the large number of *T. hamiltonii* caught in seine nets during the wet period had lengths as low as 23 mm, consistent with the October-December peak in spawning for this species elsewhere in northern Australia (Robertson & Duke, 1990b; Hoedt, 1992). In contrast, the *T. hamiltonii* that contributed to gill net

catches during the dry period typically measured between 200-230 mm, lengths not attained until *ca* 18 months of age when this species has become mature (Hoedt, 1992).

As for *T. hamiltonii*, the use of seine and gill nets in unvegetated waters at Eighty Mile Beach resulted in both the juveniles and adults of the two polynemids, *P. macrochir* and *E. tetradactylum,* being caught, suggesting that these species complete their life cycle in nearshore waters. Although the fact that no very small juveniles of *P. macrochir* were collected from shallow, nearshore waters at Eighty Mile Beach, or either of the other locations, suggests that this species may initially occupy another habitat, further intensive sampling at Anna Plains (19°21′ S, 121°19′ E) resulted in the capture of large numbers of small *P. macrochir* demonstrating that this species, like *E. tetradactylum,* uses nearshore waters as a nursery area (see Chapter 5).

The large overall difference in the species compositions of seine and gill net samples highlights the biases involved with the two methods and illustrates the importance of using a combination of sampling methods when undertaking ichthyofaunal surveys in nearshore waters. Despite the marked influence of sampling method on the species compositions in unvegetated nearshore waters, two-way ANOSIM revealed that the ichthyofauna was also influenced by sampling location.

The nMDS plot shown in Figure 4.5 demonstrated that the extent of the locational influence was similar, irrespective of sampling method. Furthermore, the samples for both seine netting and gill netting in unvegetated waters underwent the similar progressive changes in species compositions from Eighty Mile Beach to Cape Keraudren to Port Smith. As discussed previously, these progressive changes in composition follow the progressive change in the environmental variables at each of these locations, from the exposed, turbid waters at Eighty Mile Beach to the protected and relatively high clear waters found at Port Smith. The similar trends demonstrate that the combination of environmental variables, and turbidity in particular, observed at these three locations have a marked but similar influence on two largely different components of the fish fauna inhabiting nearshore waters along the Canning coast.

5. Reproductive biology of *Eleutheronema tetradactylum* and *Polydactylus macrochir*

5.1. Introduction

The sustainable management of a fish stock requires reliable data on certain crucial aspects of the biology of the target species, of which reproduction is often especially important. For example, the length and age at maturity of a species is frequently used by fisheries managers for setting minimum legal lengths for retention, which will help ensure that a substantial number of individuals of the stock has had the opportunity to spawn at least once before potentially becoming recruited into the fishery (Hill, 1990; Winstanley, 1990). Failure to appreciate the effect of consistently targeting the individuals of a species before they become mature can lead to a rapid decline in the fishery for that species (Hutchings, 2000; Frank & Brickman, 2001).

When considering if a period of fishing closure would help conserve the stocks of a species, managers require a sound understanding of the timing and duration of the spawning period of that species (Beets & Friedlander, 1999; Kritzer, 2004; Govender *et al*., 2006). Similarly, when evaluating the suitability of marine protected areas as a fisheries management tool, it is crucial for managers to know whether the spawning of key species is restricted to particular habitats and if those species undergo spawning-related migrations and/or form site-specific spawning aggregations (Domeier & Colin, 1997; Beets & Friedlander, 1999; Jamieson & Levings, 2001; Pajaro *et al*., 2005).

Reliable data are required for the above reproductive variables for both gonochoristic species and those which undergo some form of sequential hermaphroditism (see for example Chapter 1.2). In the case of hermaphroditic species, it is important not only to have reliable data on the size and age at maturity but also the sizes and ages over which such species change sex. The acquisition of these types of data for hermaphroditic species are especially relevant because fishing pressure is typically biased toward the larger individuals in a population (Berkeley *et al*., 2004; Williams & Shertzer, 2005), and thus fishing-related mortality may be disproportionately greater for the "terminal" sex (Birkeland & Dayton, 2005). For example, in protandrous species, *i.e.* those that change from male to female, it is the larger and older females that will be subjected to the greatest

fishing mortality (Milton *et al*., 1998; Blaber *et al*., 1999). High levels of exploitation may thus have a particularly detrimental effect on the total egg production by protandrous species, which has the potential to lead to recruitment overfishing (Blaber *et al*., 1996, 1999; Friedlander & Ziemann, 2003; Ley & Halliday, 2004). For this reason, it is crucially important that the development of management plans for sustaining the stocks of hermaphroditic species is based on a thorough understanding of the implications of the sizes and ages at which maturity is attained and sex change occurs (Buxton, 1992; Hesp *et al*., 2004; Alonzo & Mangel, 2005; Blaber *et al*., 2005; Heppell *et al*., 2006). The collapse of the fisheries for a number of threadfin species (Polynemidae) has been attributed to a failure to recognise or appreciate the implications of the protandrous life history of these species (Bensam & Menon, 1994; Friedlander & Ziemann, 2003; Poepoe *et al*., 2003).

Early studies of the reproductive biology of the Blue Threadfin *Eleutheronema tetradactylum* concentrated on populations in India where this species is gonochoristic and individuals with bisexual gonads rarely occur (Patnaik, 1967, 1970; Gopalakrishnan, 1972). Chao *et al*. (1994) showed that the length-frequency distributions of the males and females of *E. tetradactylum* in Singaporean waters did not differ conspicuously and thus, even though they found a large number of bisexual individuals, still concluded that that this species was unlikely to be protandrous. In contrast, on the basis of differences in the length- and age-frequency distributions of males and females and a histological examination of the gonads, Stanger (1974) concluded that, in eastern Queensland, *E. tetradactylum* was protandrous and that sex change typically took place during the second or third years of life. Stanger (1974) hypothesised that the transition from male to female in *E. tetradactylum* was initiated after the spawning season and took a year or longer to complete. However, he was unable to confirm that hypothesis as samples were not collected from throughout the year. Similarly, as Russell (1988) and McPherson (1997) collected very few samples during the summer months when this species is assumed to spawn, they were likewise unable to determine the period required for sex change. The importance of obtaining representative samples throughout the year, when exploring patterns of hermaphroditism in fishes, has been emphasised by Sadovy & Shapiro (1987).

Russell (1988), who sampled commercial catches of the King Threadfin *Polydactylus macrochir* in the Gulf of Carpentaria, was the first to report individuals of this species with bisexual gonads. Differences in the modes in the length-frequency distributions for the males and females of *P. macrochir* led both Garrett (1992) and McPherson (1997) to consider that *P. macrochir* is protandrous. However, their studies included neither histological investigations of the gonads nor large samples of fish from within the spawning season.

Estimates of the lengths at which *P. macrochir* reach maturity or change sex vary markedly. For example, the fork lengths at which the males of *P. macrochir* have been estimated to reach maturity in the Gulf of Carpentaria ranged from as low as *ca* 280 mm (McPherson, 1997) to as high as 600-800 mm (Garrett, 1992). Indeed, no study has applied logistic regression analysis to determine the L_{50} and its confidence limits for maturity for either *P. macrochir* or *E. tetradactylum*.

The results of allozyme and mitochondrial DNA studies carried out by Keenan (1997) and Chenoweth & Hughes (2003) in Queensland and the Northern Territory demonstrate that populations of both *P. macrochir* and *E. tetradactylum* exhibit genetic differences over relatively small distances (<100 km) and are likely to have distinct population structure. Thus, the marked variations in the reproductive characteristics recorded for both of these two species may reflect genetic differences among populations. Although no studies of population structure for either *P. macrochir* or *E. tetradactylum* have included samples from Western Australian populations, in view of genetic differences among populations of these two species in other parts of Australia, it is particularly important for managers to possess data on the reproductive biology of Western Australian populations of *E. tetradactylum* and *P. macrochir*. This information is required by managers for producing valid stock assessment models, which can then be used to develop appropriate policies for conserving the stocks of these species in Western Australian waters.

The overall aim of this chapter of the thesis was to obtain the first quantitative data on crucial aspects of the reproductive biology of *E. tetradactylum* and *P. macrochir* in Western Australia. The individual aims were as follows and the same for both species. 1. Confirm that these threadfins are protandrous hermaphrodites in Western Australia.

2. Determine the lengths and ages at which sex change occurs. 3. Determine the length and age at which maturity is attained. 4. Ascertain the timing and duration of the spawning period and whether fecundity is determinate or indeterminate and if spawning occurs on several occasions during a spawning period.

5.2. Methods

5.2.1. Study site and sampling regions

The seine net and gill net samples obtained from nearshore, shallow waters at Port Smith, Eighty Mile Beach and Cape Keraudren (see Chapter 2.1) provided the main source of individuals for the studies of the biology of the Blue Threadfin *Eleutheronema tetradactylum* and the King Threadfin *Polydactylus macrochir*, *i.e.* reproductive biology (this Chapter) and age, growth and mortality (Chapter 6). However, they were supplemented by samples collected from other regions by the same methods and from commercial and recreational fishers (see below), thereby enabling elements of the biology of each threadfin species in different geographical regions, *i.e.* Derby (King Sound), Roebuck Bay (Broome), Anna Plains (northern Eighty Mile Beach), Eighty Mile Beach (Wallal Station) and Cape Keraudren, to be compared.

The northernmost site sampled for threadfin was King Sound near Derby (17°00′ S, 123°00′ E) **(Figure 5.1)**. King Sound is separated from the sites sampled on the Canning coast to the south by the Dampier Peninsula **(Figure 5.1)** and the hydrology and geology of the sound are more characteristic of other Kimberley bioregions to the north than of the Canning coast (Chapter 1, IMCRA, 1998). King Sound experiences the greatest tidal movement in Australia (*ca* 11 m during spring tides). This large tidal movement and the fact that the Fitzroy River is very large and discharges into King Sound results in the waters of the sound being constantly turbid, particularly during spring tides (Pepping *et al*., 1999).

Roebuck Bay is located immediately to the south of Broome at (18°10′ S, 121°19′ E). Samples of threadfin were collected from the southern part of the bay, where the foreshore contains a band of mangroves, including *Rhizophora stylosa, Avicennia marina*, *Ceriops tagal* and *Bruguiera exaristata*, that extend above extensive, muddy,

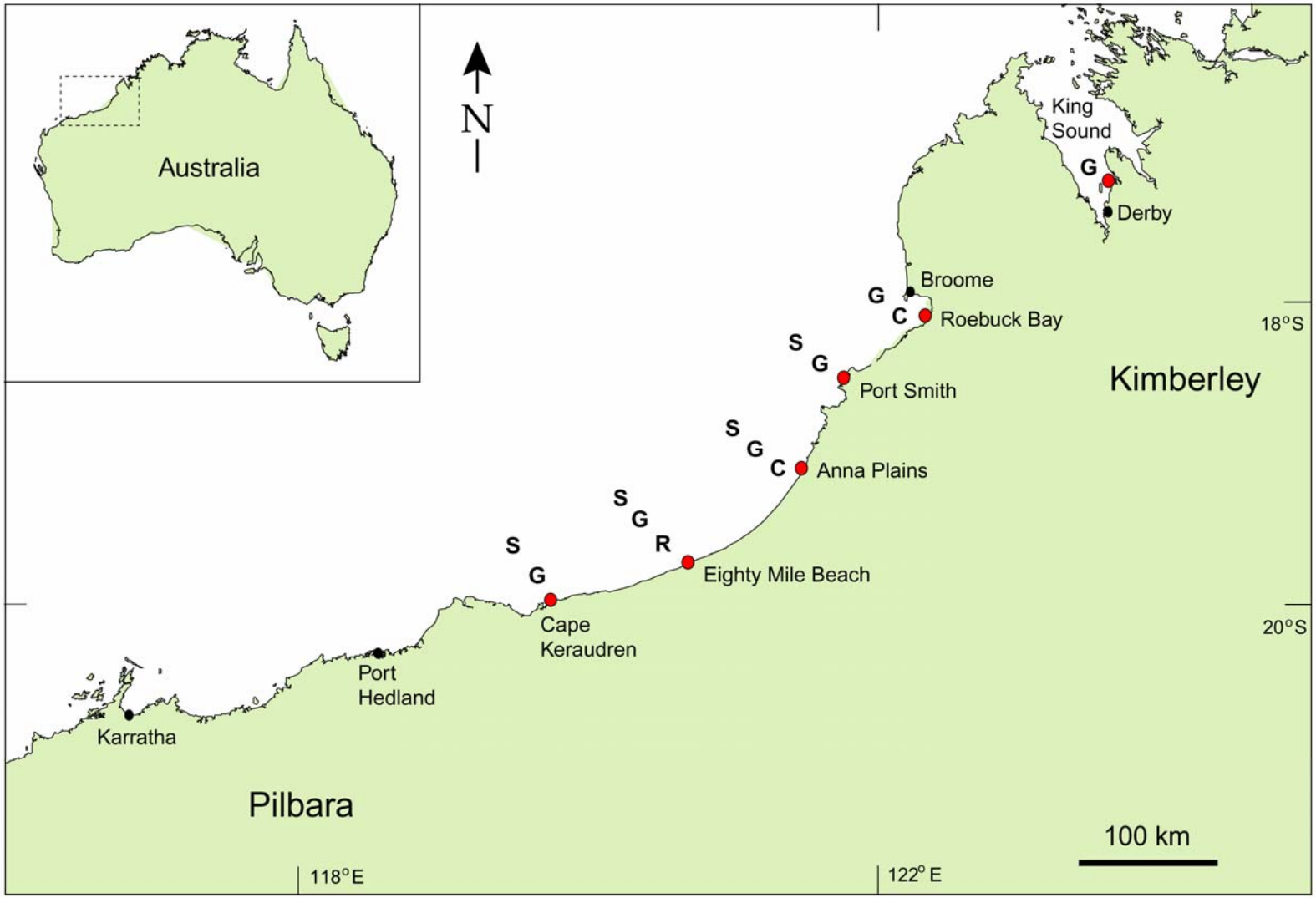

Figure 5.1. Map of north-western Australia showing locations (●) where the Blue Threadfin *Eleutheronema tetradactylum* and the King Threadfin *Polydactylus macrochir* were sampled. The letters S, G, C and R refer to where samples were collected using seine or gill nets and from commercial and recreational fishers, respectively.

flats. These flats have a very high concentration of invertebrates and are one of the three most important migratory bird habitats in Australia, with, at any one time, the number of species and numbers of individuals of waders in Roebuck Bay often in excess of 50 and 140 000, respectively (Piersma *et al*., 2002)

The nearshore habitat found at Anna Plains (19°21′ S, 121°19′ E) at the northern end of Eighty Mile Beach, *ca* 200 km south of Broome **(Figure 5.1)**, is very similar to that found at Wallal Station to the south (see Chapter 2.2.1). The main difference is that the beach has a more westerly orientation, consists of slightly finer, silty sediments and has an even slighter gradient, exposing up to 3000m of sand flat on low spring tides. Intertidal mud flats in this region also have a very high diversity of macrobenthos and comprise important shorebird habitat (Piersma *et al*., 1999; Wade, 2004).

5.2.2. Sampling regime

Seasonal samples of both threadfin species were extracted from the samples collected at Port Smith, Eighty Mile Beach and Cape Keraudren between December 2000 and November 2002 using the 60.5 m seine net and composite gill net for the study of the fish communities at those locations (see Chapter 2.1.2). The collection of seasonal samples of threadfin with the 60.5 m seine net and composite gill net continued at Eighty Mile Beach until late 2004. The composite gill net was also used to collect samples of *P. macrochir* from King Sound, near Derby, on five occasions between June 2002 and November 2003. Occasional samples of both *E. tetradactylum* and *P. macrochir* were also collected throughout the study from each region using rod and line and a monofilament throw net. The throw net, which had a diameter of *ca* 2.4 m and was constructed of 10 mm monofilament mesh, was deployed in shallow (<0.5 m) nearshore waters that were free of obstructions before being dragged on to the shore.

Threadfin were also collected from recreational and commercial fishers. Although recreational fishers predominantly target both species of threadfin using rod and line **(Plate 5.1)**, recreational haul netting was also permitted during the study period. Haul nets, which had a mesh of between 80 and 100 mm, were 30 m long and constructed of monofilament. The majority of recreational haul netting in the region was undertaken

Plate 5.1. Photograph looking east from the caravan park at Eighty Mile Beach, showing more than 50 recreational fishers targeting threadfin in a 1 km stretch of beach.

Plate 5.2. Photograph of the intertidal flat at low tide at Anna Plains, showing a staked commercial gill net awaiting inundation.

close to Wallal Station on Eighty Mile Beach (**Figure 5.1**). Regulations on the recreational use of haul nets in Western Australia have recently been reviewed and, as a result, this method can no longer be used to target threadfin species in north-western Australia (see Anon., 2005).

Commercial fishers target threadfin in nearshore waters with heavy gauge monofilament gill nets. Gill nets are either set from boats in shallow tidal waters that are typically less than 1 m deep, *i.e.* at Roebuck Bay, Broome, or staked or anchored at low tide on the foreshore perpendicular to the water and which subsequently become inundated by the incoming tide, *i.e.* at Anna Plains **(Plate 5.2)**. Although individual gill nets are typically *ca* 60 m long, up to 1000 m of net may be used at any time. During the present study, commercial fishers at Roebuck Bay and Anna Plains fished exclusively with gill nets that had stretched mesh widths of 140 mm and 165 mm, respectively.

Commercial gill net fishers in north-western Australia are presently subjected to a closed fishing season during December and January, which is aimed at protecting Barramundi *Lates calcarifer* during its spawning period. Thus, as commercial samples of threadfin were not available from both Roebuck Bay and Anna Plains during December and January, the composite gill net was used during this period to collect samples of threadfin from both of those locations.

5.2.3. Habitats of threadfin

The seasonal sampling regime, which employed the 60.5 m seine net and composite gill net at Port Smith, Eighty Mile Beach and Cape Keraudren (Chapters 3, 4), produced data on the seasonal abundance and habitats of *E. tetradactylum* and *P. macrochir.* To further refine the understanding of habitat use by the juveniles of *E. tetradactylum* and *P. macrochir*, six replicate samples were collected during spring from Anna Plains, Port Smith, Eighty Mile Beach and Cape Keraudren using a 21.5 m seine net. Note that the prevalence of estuarine crocodiles in King Sound and the extremely soft sediment in Roebuck Bay made it unfeasible to seine net at these two locations.

The 21.5 m seine net used during this study consisted of two 10 m long wings and a 1.5 m bunt. Each wing consisted of a 6 m panel of 9 mm mesh and a 4 m panel of 3 mm

mesh, while the bunt had a mesh of 3 mm. The net fished to a depth of 1.5 m and covered a total area of *ca* 116 m^2. The net was walked out from the beach and extended parallel to the shore and then dragged towards the shoreline, *i.e.* in the same manner as the 60.5 m long seine net (see Chapter 2.2.1).

The numbers of *E. tetradactylum* and *P. macrochir* in each replicate sample collected with the 21.5 m seine net were converted to densities, *i.e*. number of individuals 100 m^{-2}. Examination of the relationship between the mean and standard deviation for the densities of both *E. tetradactylum* and *P. macrochir* showed that, prior to subjection to analysis of variance (ANOVA), the densities of both species should be $\log_{10}$ (n+1) transformed (see Chapter 3.2 for rationale). One-way ANOVA was then used to determine if the densities of both *E. tetradactylum* and *P. macrochir* were significantly different between regions, *i.e.* Anna Plains and Eighty Mile Beach. Note that no juvenile threadfin were caught with the 21.5 m seine net at either Port Smith or Cape Keraudren.

5.2.4. Gonadal staging and histology

Each threadfin collected using seine, gill and throw nets and rod and line or obtained from commercial or recreational fishers was measured to the nearest mm (total length and fork length) and weighed to the nearest 0.1 g. The ways in which the two threadfin species were processed for determining their age compositions and growth and mortality estimates are given in Chapter 6.2. The gonads of each threadfin (>*ca* 50 mm TL) were removed and weighed to the nearest 0.01 g and the sex of each fish was recorded when the gonad consisted entirely of either testicular or ovarian tissue. Gonads were macroscopically assigned to one of the following maturity stages that were based on those described by Laevastu (1965). I = virgin (males only); II = immature/resting; III = developing; IV = maturing; V = mature/pre-spawning; VI = spawning; VII = spent; VIII = recovering (see Chapter 5.3.3). For those fish < 50 mm, gonads were observed under a dissecting microscope. When the sex of fish < 50 mm could not be ascertained, that individual was recorded as unsexed.

When both testicular and ovarian tissues were observed in the gonad of a fish, that fish was recorded as having bisexual gonads. The gonads of each bisexual fish were

removed and weighed and their testicular and ovarian components were each assigned to one of the above maturation stages. The mid-region of each bisexual gonad was cut transversely and the cross-sectional areas of its testicular and ovarian components were then estimated subjectively. This enabled the approximate percentage contributions of each of those components to be calculated. The precise cross-sectional area of the testicular and ovarian components for a sub-sample of fish with bisexual gonads was measured from histological preparations using the Leica computer image managing package, IM1000, after the images had been recorded employing a Leica DC 300 video camera attached to a Leica MZ 7.5 dissecting microscope. These precise percentage contributions of the testicular and ovarian components of bisexual gonads typically differed by < 5% from those subjective estimates obtained macroscopically. N.B. Preliminary studies demonstrated that, in bisexual gonads, the proportions of each component were similar throughout the length of both gonadal lobes. The gonads of bisexual fish could then be categorised as predominantly testis (consisting of ≥ 2/3 testicular tissue), equal testis and ovary (consisting of 1/3 to 2/3 testicular tissue) or predominantly ovary (consisting of ≤ 1/3 testicular tissue).

Each month, the gonads from a wide size range of male, female and bisexual individuals, and some unsexed individual with total lengths < 50 mm, were collected and placed in Bouin's fixative for between 24 and 48 h, depending on their size, and then dehydrated in an ascending series of ethanol concentrations. A part of the mid-region of one of the gonad lobes was embedded in paraffin wax and cut transversely into 6 μm sections and stained with Mallory's trichrome. The sections were used to validate the macroscopic staging of the gonads, to allow a detailed investigation of the pattern of protandrous sex inversion (see results) and to determine whether female threadfin salmon had determinate or indeterminate fecundity.

5.2.5. Length at maturity and sex change

As *E. tetradactylum* and *P. macrochir* in Western Australia were later shown to be protandrous (see results and discussion), *i.e.* start life and mature as males and later change sex to females, the lengths at which 50% of individuals attain maturity (L_{50}), were

determined for the males of these two species. The L_{50}s were calculated, using logistic regression analysis, to determine the relationship with total length of the probability of a fish being mature during the spawning season. All fish with gonads at stages III-IV were assumed to have had the potential to become fully mature during the spawning season and are thus considered to be "mature" for the purposes of this calculation, while those with gonads at stages V - VIII would already have become mature during that spawning season. The form of the logistic equation is $P = 1/\{1+\exp[-\ln(19)(L-L_{50})/(L_{95}-L_{50})]\}$, where P = probability that a male is mature, L = total length, L_{50} and L_{95} = the lengths at which 50 and 95% of male fish reach sexual maturity, respectively, and ln = the natural logarithm.

The data (immature or mature) for individual fish were randomly resampled and analysed to create 1000 sets of bootstrap estimates for the parameters of the logistic regression and estimates of the probability of maturity within the range of recorded lengths. The 95% confidence limits of the L_{50}s and L_{95}s, derived using this resampling technique, were taken as the 2.5 and 97.5 percentiles of the corresponding predicted values resulting from this resampling analysis. The point estimates for each parameter and of each probability of maturity at the specified length were taken as the medians of the bootstrap estimates.

The length at which 50% of the individuals of both *E. tetradactylum* and *P. macrochir* had changed sex from male to female was determined using the same methodologies as for length at maturity. For both species, the L_{50}s at sex change were calculated using logistic regression analysis, where P = the probability that a fish had changed from male (or a transitional, *i.e.* bisexual state) to female. Thus, the males and transitional fish were grouped together for this analysis and the L_{50}s derived correspond to the length at which 50% of individuals have completed sex change. For each species, the above analysis was conducted separately using data derived for fish sampled in four different regions, namely Roebuck Bay, Anna Plains, Eighty Mile Beach and Cape Keraudren in the case of *E. tetradactylum*, and Derby, Roebuck Bay, Anna Plains and Eighty Mile Beach with *P. macrochir*. Likelihood-ratio tests (Cerrato, 1990) were used to determine whether both the L_{50} and L_{95} values derived for each species for length at sex change differed among regions.

In an attempt to explore regional variations in the timing of sex change in *P. macrochir*, logistic regression analysis using the above resampling procedure and the ages at capture was used to determine the age at which that species undergoes sex change in each region. The age of each individual *P. macrochir* used in the age at sex change analyses are derived from the results of Chapter 6. The A_{50} and A_{95} values derived from this analysis for *P. macrochir*, grouping males and transitional fish, correspond to the age at which 50 and 95% of individuals have completed sex change, respectively.

As the length at which *E. tetradactylum* changed sex did not vary conspicuously among regions (see results), the above logistic regression analysis was repeated using the data from the four pooled regions to determine overall L_{50} and L_{95} values for the completion of sex change for that species. Furthermore, because there were substantial numbers of transitional *E. tetradactylum*, it was possible also to use the same logistic procedure to estimate the lengths at which sex change commences by grouping fish containing transitional gonads with females, with *P* now = the probability that a fish has changed from male to a transitional state (or become a female). Fish from all months of the year were included in the above analysis to determine the L_{50}s + L_{95}s and A_{50}s + A_{95}s corresponding to the commencement and completion of sex change. As for *P. macrochir,* the ages of individual *E. tetradactylum* used in the age at sex change analyses are derived from the results of Chapter 6.

Note that low sample sizes, at some locations, of *E. tetradactylum* and *P. macrochir* males that had lengths that were near the size at sexual maturity required that the data from the different locations be pooled to determine an overall length at maturity for each species in north-western Australia. Similarly, the analyses described below for determining the period and frequency of spawning in both species of threadfin was also conducted using data from the pooled locations.

5.2.6. Spawning period and frequency

The gonadosomatic index (GSI) of each individual of *E. tetradactylum* and *P. macrochir* was calculated from the equation GSI = W1/(W2-W1) x 100, where W1 = wet weight of the gonad and W2 = wet weight of whole fish. A combination of the trends exhibited by

the mean monthly GSIs and the monthly proportions of each gonadal stage of males and females of *E. tetradactylum* and *P. macrochir* were then used to determine the time of peak spawning and the duration of the spawning period of the two species. In the case of bisexual fish, visual estimates of the proportions of the testicular and ovarian components were used, in conjunction with the total weight of that gonad and of the fish, to derive approximate GSI values for both of those gonadal components.

The circumferences of 100 oocytes from histological sections of the ovaries of two spawning females (stage VI) of each species were measured to the nearest 0.01 μm. Measurements, which were restricted to oocytes that had been sectioned through their nuclei, were obtained using the Leica computer image managing package, IM1000, using the same system described earlier. This allowed the diameters of each type of oocyte in each ovary to be calculated and resultant distribution of the diameters within the overall oocyte diameter frequency distributions to be used to elucidate the type of fecundity of each species, *i.e*. determinate or indeterminate (Hunter & Macewicz, 1985; Hunter *et al*., 1985).

5.3. Results

5.3.1. Length and age distributions of the different sexes

The vast majority of the paired gonads of the 1348 *Eleutheronema tetradactylum* (85.3%) and the 1662 *Polydactylus macrochir* (96.0%) that were examined could be designated macroscopically as comprising solely either testicular or ovarian tissue and were able to be assigned a maturity stage. Thus, when the individuals of these two species possessed well-defined gonads, they could typically be identified as male or female and the stage in development of their gonads determined (**Plate 5.3a, b**). Histological sections of the gonads of a random subsample of approximately 20 such fish in each month were used to confirm that these fish contained exclusively either testicular or ovarian tissue. However, the gonads of some individuals of *E. tetradactylum* (14.7%) and *P. macrochir* (4.0%) were bisexual, *i.e.* contained both testicular and ovarian tissue (**Plate 5.3c**), the ratios of which varied markedly. In a few cases, the minor component was barely detectable, *i.e*. contributed < 5% of the gonad. All such gonads, which did not have the typical

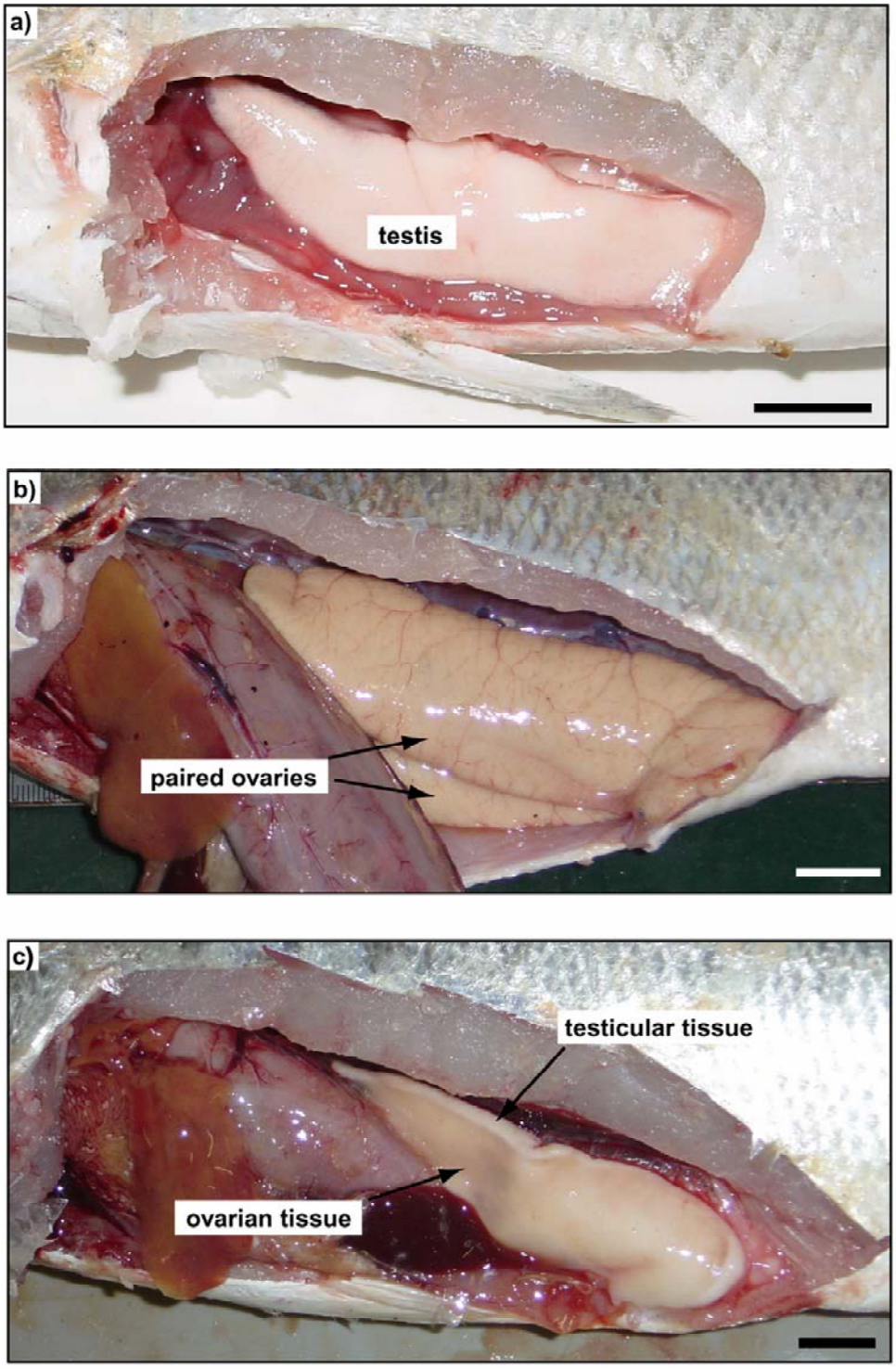

Plate 5.3. Macroscopic view of a) mature (stage V) testes from *Polydactylus macrochir* (306 mm TL) and b) mature (stage V) ovaries from *Eleutheronema tetradactylum* (520 mm TL) and c) bisexual gonads from *E. tetradactylum* (356 mm TL) consisting of *ca* 2/3 testicular (stage V) and *ca* 1/3 ovarian (stage II) tissue. Scale bars in (a), (b) and (c) = 10, 15 and 10 mm, respectively.

macroscopic appearance of a testis or an ovary, *i.e*. were atypically pink or possessed a thin white strand on their dorsal surface, were preserved for microscopic examination. Subsequent examination of the histological sections demonstrated that this "type" of gonad contained both testicular and ovarian material.

The sex of some small threadfin individuals, *i.e.* those < *ca* 50 mm TL, was unable to be distinguished macroscopically due to the small size of the gonads. Examination under a dissecting microscope demonstrated these individuals were immature males. Furthermore, histological preparations of gonads from very small individuals of either species revealed these small fish to be males and there was no evidence of ovarian material in any gonads. As such, threadfin < 50 mm originally recorded as "unsexed" have been labelled as males for the purposes of maturity and sex change analyses.

The lengths of *E. tetradactylum* obtained using all sampling methods ranged from 20 to 793 mm, with those of males, *i.e*. 20 to 413 mm ($\bar{x}$ = 119 mm), showing limited overlap with those of females, *i.e*. 330 to 793 mm ($\bar{x}$ = 486 mm). The length range of the bisexual fish, which contained both testicular and ovarian tissue, *i.e*. 279 to 455 mm ($\bar{x}$ = 370 mm), lay at the upper end of that for males and at the lower end of that for females (**Figure 5.2a**). All *E. tetradactylum* in their first year of life were males and virtually all of those in their fourth and subsequent years of life were females (**Figure 5.2b**). Fish containing bisexual gonads were almost entirely restricted to the 1+ and 2+ age classes to which they contributed 11.6 and 41.2%, respectively (**Figure 5.2b**).

The lengths of *Polydactylus macrochir* collected using all methods ranged from 19 to 1393 mm, with the lengths of males ranging from 19 to 1159 mm ($\bar{x}$ = 558 mm) and those of females from 440 to 1393 mm ($\bar{x}$ = 878 mm). In contrast to the situation with *E. tetradactylum,* in which fish containing bisexual gonads were concentrated in a relatively narrow length range, the lengths of bisexual *P. macrochir* ranged widely from 313 to 1139 mm ($\bar{x}$ = 723 mm) and typically never contributed > 10% to the fish in any 50 mm length class (**Figure 5.3a**). All 0+ fish and virtually all 1+ *P. macrochir* were males. Males contributed to all age classes up to and including the 7+ age class and comprised *ca* 90% of all *P. macrochir* less than 5 years old (**Figure 5.3b**). Small numbers of bisexual fish were found in each age class between 1+ and 7+. Females first appeared in the 1+ age class, but only in small numbers, and reached their highest number (56) in the

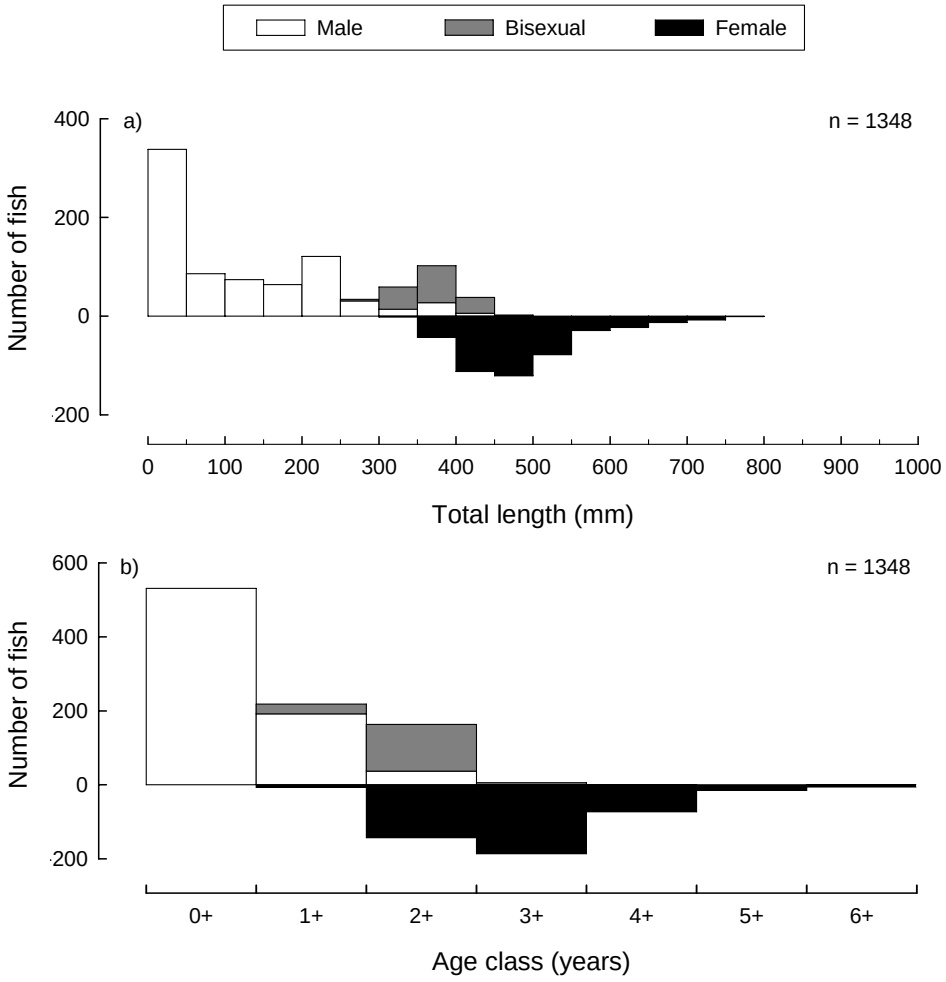

Figure 5.2. a) Length-frequency and b) age-frequency distributions for male, bisexual and female individuals of *Eleutheronema tetradactylum* caught with seine and gill nets and by recreational and commercial fishers in north-western Australia.

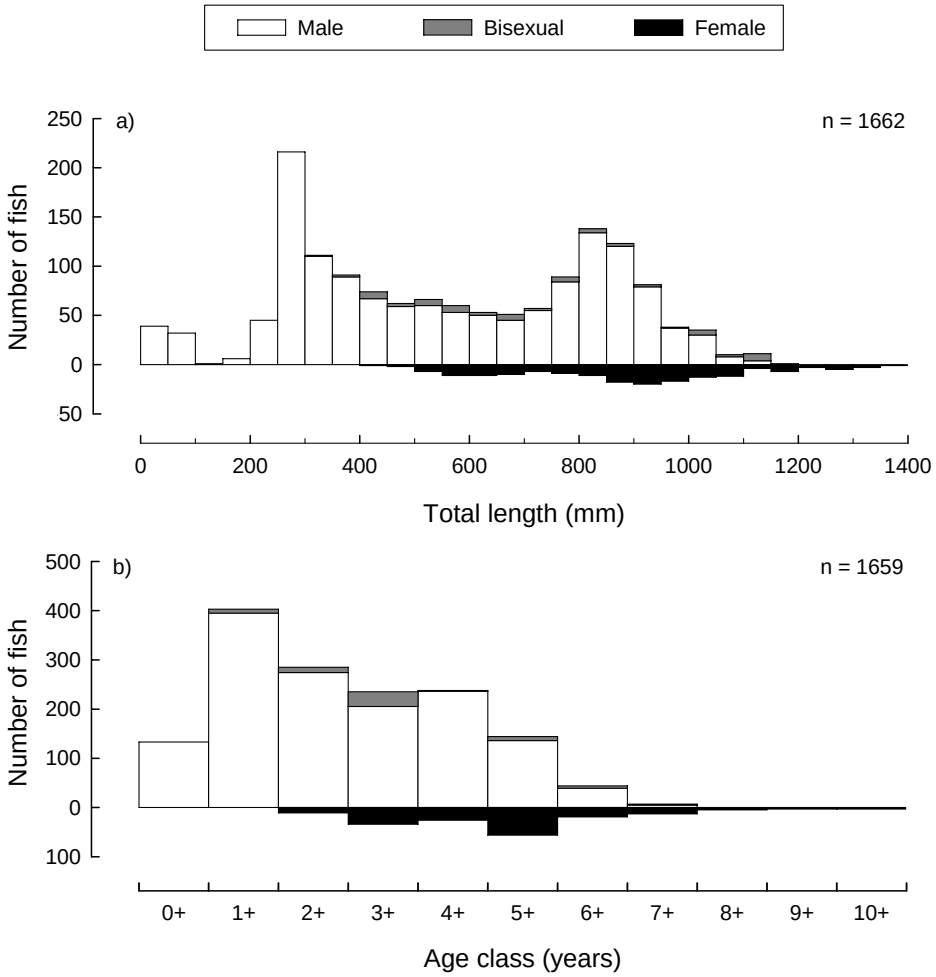

Figure 5.3. a) Length-frequency and b) age-frequency distributions for male, bisexual and female individuals of *Polydactylus macrochir* caught with seine and gill nets and by recreational and commercial fishers in north-western Australia.

5+ age class. All of the 11 individuals in the 8+ to 10+ age classes were females (**Figure 5.3b**).

5.3.2. Characteristics of testes, ovaries and bisexual gonads

The macroscopic characteristics of the different stages in the development and maturation of the definitive testes and ovaries of *E. tetradactylum* and *P. macrochir*, together with the cytological characteristics of each of those stages are presented in **Tables 5.1 and 5.2** and illustrated in **Plates 5.4 and 5.5.** A thorough examination of histological sections of the gonads of both species demonstrated that the testes and ovaries of *E. tetradactylum* and *P. macrochir* develop and mature in essentially the same way.

Although the ratios of testicular to ovarian tissue varied markedly in bisexual gonads, the gonadal components were always situated in the same regions of the gonads, with the testicular tissue located along the dorsal and inner lateral regions of the paired gonads, whereas the ovarian tissue lies in the ventral and outer regions (**Plate 5.3c**). In each bisexual gonad, the testicular and ovarian components are separated by well developed connective tissue. The structure of each gonad and the ratio of testicular to ovarian tissue is essentially the same along the full length of each gonad. Bisexual gonads could be categorised, on account of the ratio of testicular and ovarian tissue, as predominantly testis (≥ 2/3 testicular tissue), near equal testis and ovary (1/3 to 2/3 testicular tissue) or predominantly ovary (≤ 1/3 testicular tissue). Within each of these three categories, the microscopic characteristics of individual gonads were similar and were essentially the same in *E. tetradactylum* and *P. macrochir*.

Bisexual gonads comprising predominantly testicular tissue

Bisexual gonads, which predominantly comprise of testicular tissue, are distinguished macroscopically from those of a typical male by having a pinkish colouration in the region of the ovarian tissue and being more rounded in cross-section than a definitive testis (**Plate 5.6a**). The microscopic characteristics of the testicular region are similar to those of a mature testis and thus typically contain a range of stages in spermatogenesis from primary spermatocytes to spermatozoa. Furthermore, the large numbers of spermatids and spermatozoa tightly packed in sperm sinuses and in the sperm duct (**Plate 5.6a, b**) suggest

Table 5.1. Characteristics of the macroscopic stages in the development of the testes of *Eleutheronema tetradactylum* and *Polydactylus macrochir*, together with their corresponding histological characteristics.

Stage	Macroscopic characteristics	Histological characteristics
I/II Immature / resting	Testes very small, grey and strand-like (stage I) to white and ribbon-like (stage II).	Dominated by large amounts of connective tissue. Stage II testes have numerous crypts containing spermatocytes, spermatids and some spermatozoa, which are present in all subsequent testicular stages.
III Developing	Testes white and occupy approximately half the length of the body cavity.	Large amounts of conspicuous connective tissue still present, crypts containing spermatozoa, spermatids and spermatozoa aggregate in sperm sinuses near the centre of the testes and close to the now conspicuous sperm duct.
IV Maturing	No milt appears when pressure is applied to the trunk of males. Occupy more than half the length of the body cavity.	Sperm duct well developed and usually full of spermatids and spermatozoa. Sperm sinuses are well developed close to sperm duct and typically occupy up to half the area of testis.
V/VI Mature / spawning	Gonads 1/3 to filling ventral cavity. Milt exuded from testes with firm pressure to abdominal region.	Sperm duct and the majority of testes are full of spermatids and spermatozoa. Often difficult to distinguish between sperm duct and sinuses. Crypts containing spermatozoa are usually confined to the outer perimeter of the testis.
VII Spent	Gonads smaller than at stage V or VI. Testes flaccid though not fully empty.	Large numbers of spermatids and spermatozoa are still obvious in sperm sinuses and duct. However, large spaces empty of sperm are also present within the connective tissue.
VIII Recovering	Testes red to brown, small and flaccid.	Testes dominated by connective tissue containing large spaces and few sperm. In contrast to previous stages, few crypts contain spermatozoa.

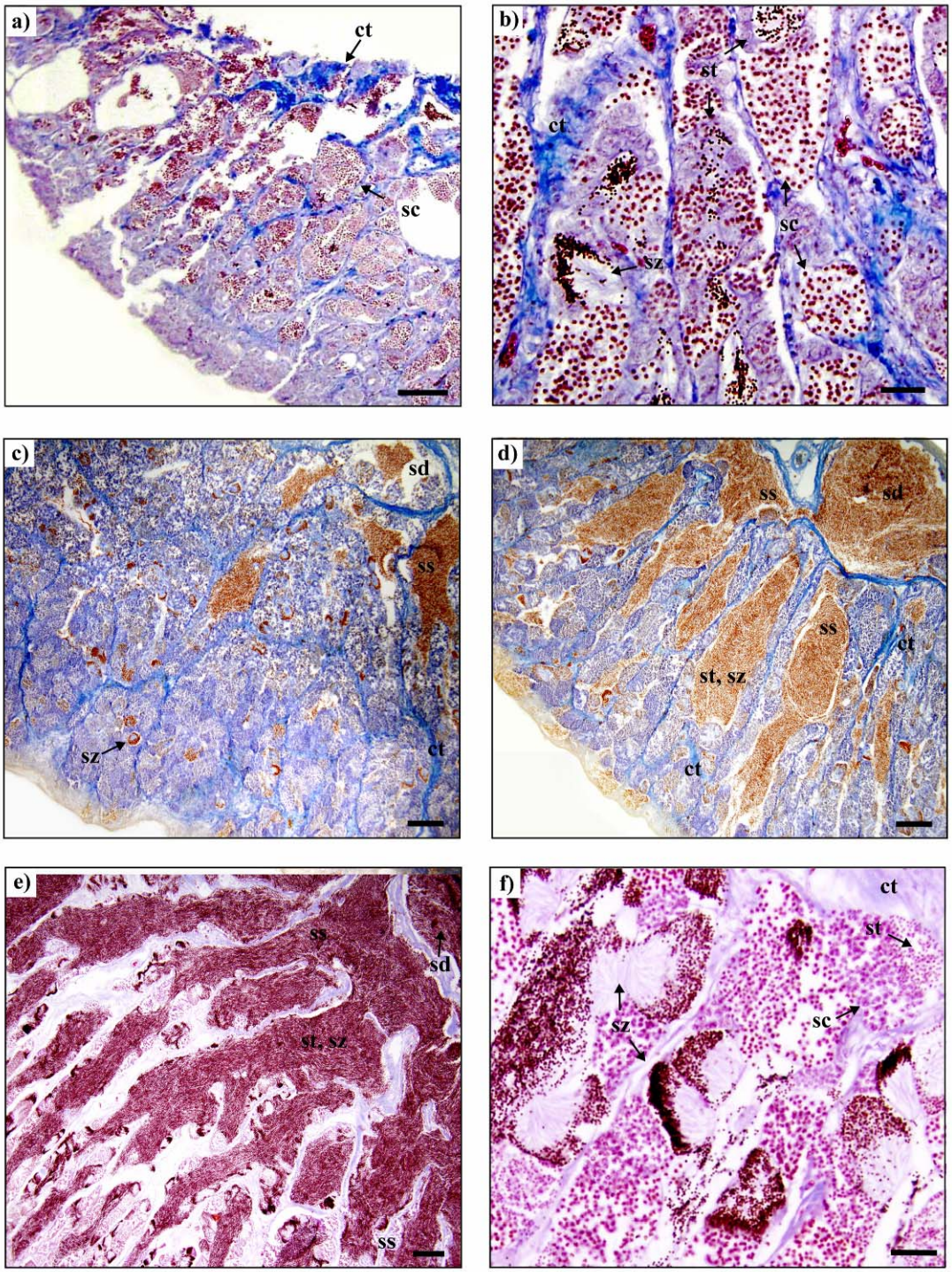

Plate 5.4. Histological sections showing selected stages in the development of the testes of the males of (a, b, e, f) *Polydactylus macrochir* and (c, d) *Eleutheronema tetradactylum*. (a-b) resting (stage II) (Aug; 626 mm TL) with minimal sperm development, (c) early developing (stage III) (Sept; 311 mm TL), (d) maturing (stage IV) (Sept; 243 mm TL) and (e-f) mature (stage V) (Oct; 383 mm TL). ct, connective tissue; sc, spermatocytes; sd, sperm duct; ss, sperm sinuses; st, spermatids; sz, spermatozoa. Scale bars (a, c-e) 100 µm; (b, f) 25 µm.

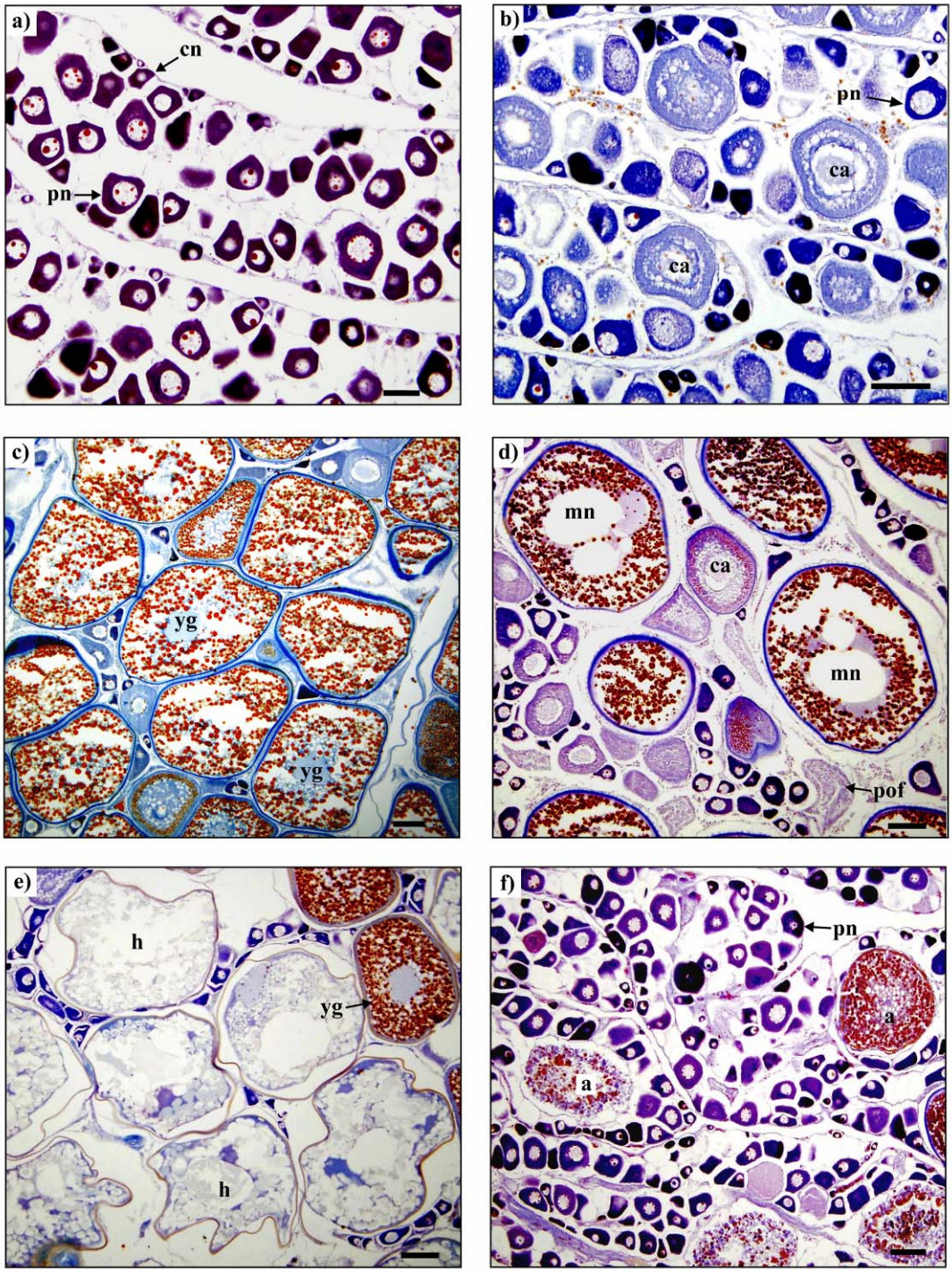

Plate 5.5. Histological sections showing selected stages in the development of the ovaries of (a, f) *Polydactylus macrochir* and (b-e) *Eleutheronema tetradactylum*. (a) resting (stage II) (Jun; 941 mm TL), (b) early developing (stage III) (Sept; 410 mm TL), (c) mature (stage V) (Sept; 525 mm TL), (d-e) spawning (stage VI) (Oct; 420 mm TL; Dec; 568 mm TL) and (f) recovering (stage VIII) (Feb; 568 mm TL). a, atretic oocyte; ca, cortical alveolar oocyte; cn, chromatin nucleolar oocyte; h, hydrated oocyte; mn, migratory nucleus oocyte; pn, perinucleolar oocyte; pof, post ovulatory follicle; yg, yolk granule oocyte. Scale bars (a) 50 µm; (b-f) 100 µm.

Table 5.2. Characteristics of the macroscopic stages in the development of the ovaries of *Eleutheronema tetradactylum* and *Polydactylus macrochir*, together with their corresponding histological characteristics. Adapted from the criteria of Laevastu (1965). Terminology for oocyte stages follows Wallace & Selman (1989).

Stage	Macroscopic characteristics	Histological characteristics
II **Immature / resting**	Small and transparent. Yellowish-orange in colour. Oocytes not visible through ovarian wall.	Ovigerous lamellae highly organised. Chromatin nucleolar oocytes dominate the complement of oocytes. Oogonia and perinucleolar oocytes sometimes present. Small previtellogenic oocytes present in all subsequent ovarian stages.
III **Developing**	Slightly larger than at stage II. Oocytes visible through ovarian wall.	Chromatin nucleolar, perinucleolar and cortical alveolar oocytes present.
V **Maturing**	Larger than stage III, occupying about half of the body cavity. Creamy orange in colour. Large oocytes visible through ovarian wall.	Cortical alveolar and yolk granule oocytes abundant.
V/VI **Mature / spawning**	Large, occupying about half to two thirds of body cavity. Extensive capillaries visible in ovarian wall. Hydrated oocytes sometimes visible through ovarian wall in stage VI ovaries. Ovaries of *P. macrochir* typically with lateral undulations anteriorly.	Yolk granule oocytes abundant. Migratory nucleus oocytes, hydrated oocytes or post-ovulatory follicles present in stage VI ovaries.
VII **Spent**	Smaller than V/VI and flaccid. Some large oocytes visible through ovarian wall.	Remnant yolk granule oocytes present, typically undergoing atresia. Some connective tissue present throughout ovaries.
VIII **Recovering**	Small, flaccid and dark red. Variations in thickness of the ovarian wall of *P. macrochir* ovaries produces a concertina appearance.	Extensive connective tissue present among ovarian lamellae.

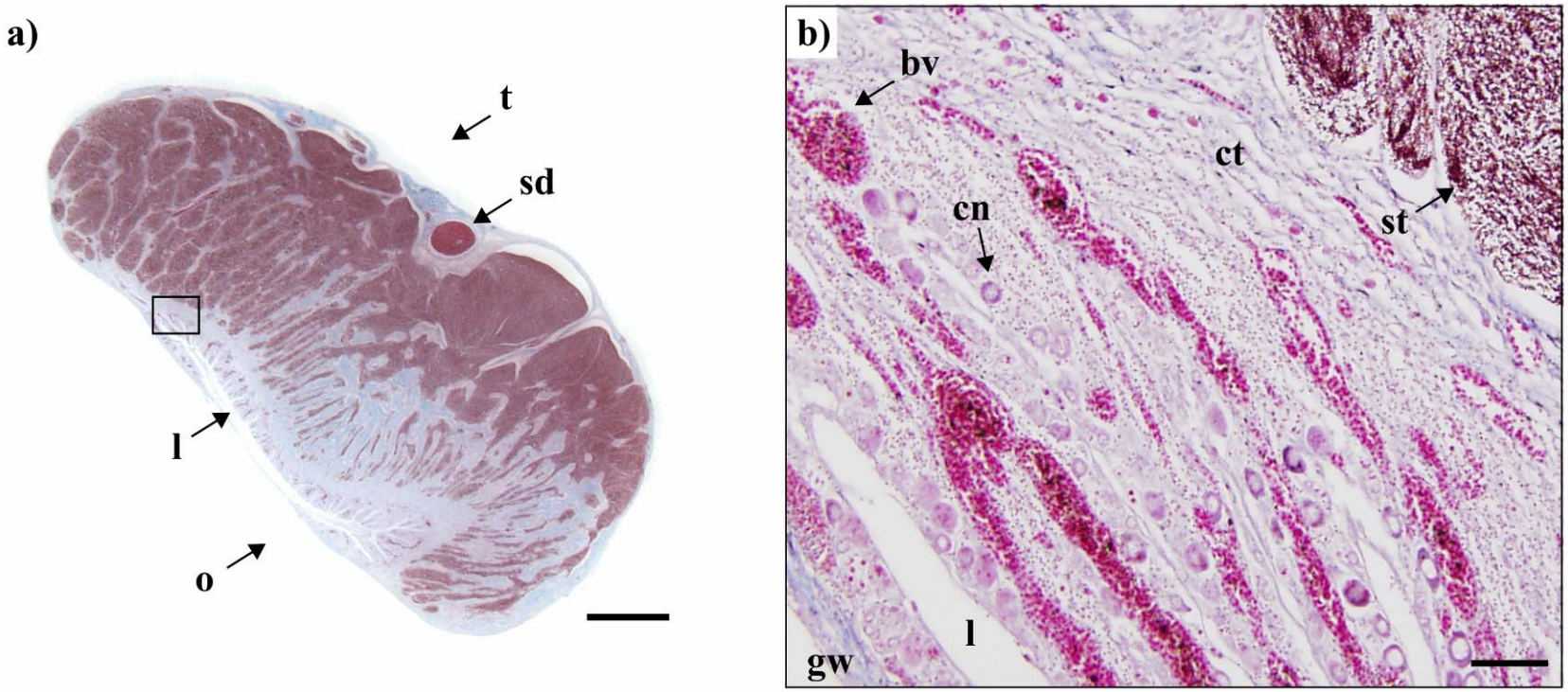

Plate 5.6. a) Low power and b) high power photographs of transverse sections through the mid-region of a bisexual gonad from *Polydactylus macrochir* (437 mm TL), which comprises predominantly testicular tissue. bv, blood vessel; cn, chromatin nucleolar oocyte; ct, connective tissue; gw, gonad wall; l, ovarian lumen; o, ovary; sd, sperm duct; st, spermatid; t, testis; Scale bars in (a) & (b) represent 500 and 50 µm, respectively.

that gonads have functioned as males. The ovarian component is categorised by a large amount of connective tissue interspersed with previtellogenic oocytes. The previtellogenic oocytes, which frequently include early oogenesis stages, *i.e.* oogonia, are located within the connective tissue which surrounds a simple luminal space. The connective tissue surrounding the previtellogenic oocytes is highly vascularised (**Plate 5.6b)**.

Bisexual gonads containing equal amounts of testicular and ovarian tissue

In bisexual gonads, where the ratio of testicular to ovarian tissue is nearly equal, the two components of the gonad are demarcated by well developed intervening connective tissue. The testicular component contains cells at a range of stages in spermatogenesis, including spermatozoa, which are contained in crypts located around the periphery of the testicular region. Although sperm sinuses are typically smaller than in the previous category of bisexual gonads, the sperm duct is still well developed and contains large numbers of spermatids and spermatozoa (**Plate 5.7a, b**). The ovarian component of the gonad is similar in appearance to the resting (stage II) ovary of female fish with previtellogenic oocytes arranged around a prominent luminal space (**Plate 5.7a)**.

Bisexual gonads comprising predominantly ovarian tissue

This type of bisexual gonad, which is dominated by ovarian tissue and assumed the appearance of a typical resting ovary, is typically round in cross-section and contains, throughout its length, evaginations projecting into the prominent lumen (**Plate 5.8a**). Most of the oocytes are at an early previtellogenic stage. The testicular component is much smaller than in the previous two categories of bisexual gonads and, in some individuals is so reduced that it occupies only a short length of the dorsal surface of the gonad. Bisexual gonads of this type typically contain no cells in the early stages of spermatogenesis, such as primary spermatocytes, and many of the crypts in the testicular region are empty. The spermatozoa present are not tightly packed and typically stain more darkly than those in the gonads of mature males, *i.e.* are pycnotic (**Plate 5.8b**). The sperm duct is not well developed, and does not typically contain large numbers of spermatozoa (**Plate 5.8a**).

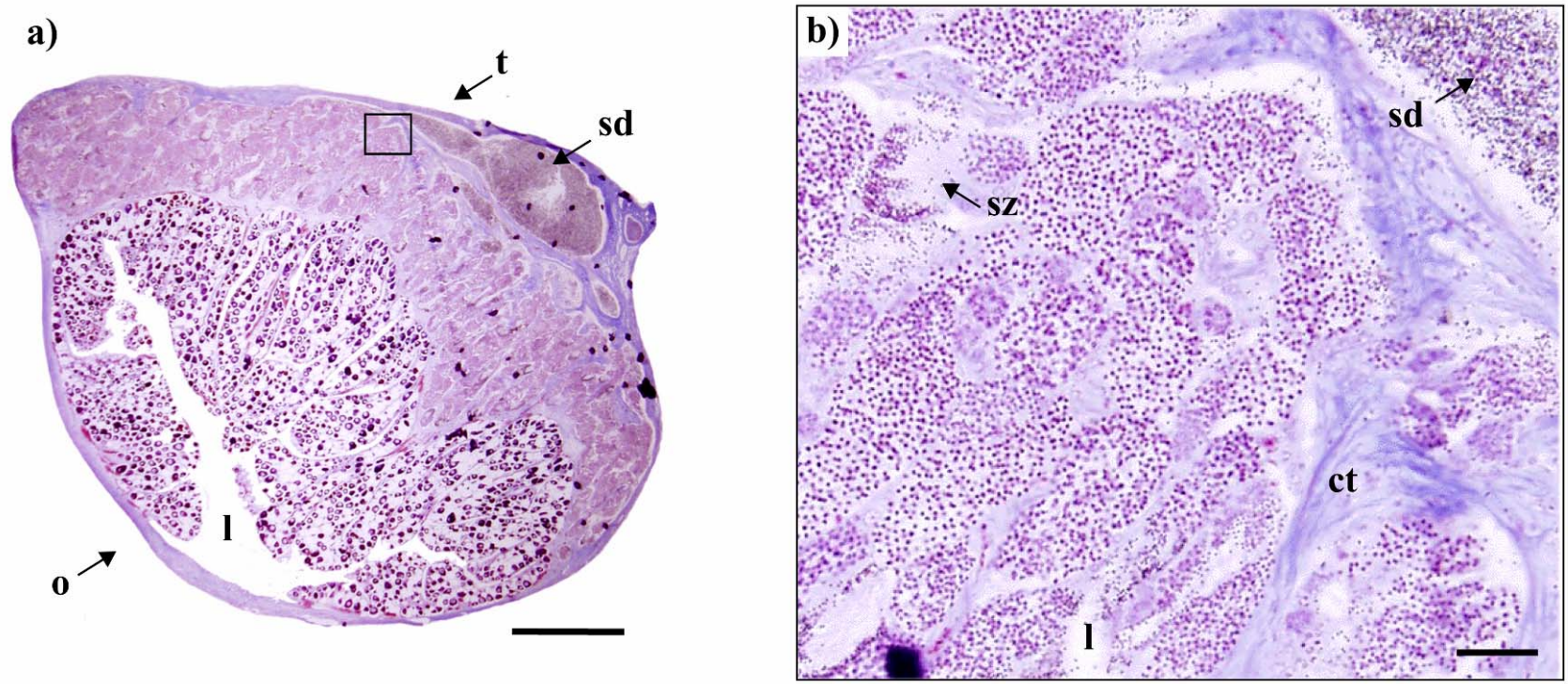

Plate 5.7. a) Low power and b) high power photographs of transverse section through the mid-region of a bisexual gonad from *Polydactylus macrochir* (313 mm TL), which is contains nearly equal amounts of testicular and ovarian tissue. ct, connective tissue; l, ovarian lumen; o, ovary; sd, sperm duct; sz, spermatozoa; t, testis; Scale bars in (a) & (b) represent 500 and 50 µm, respectively.

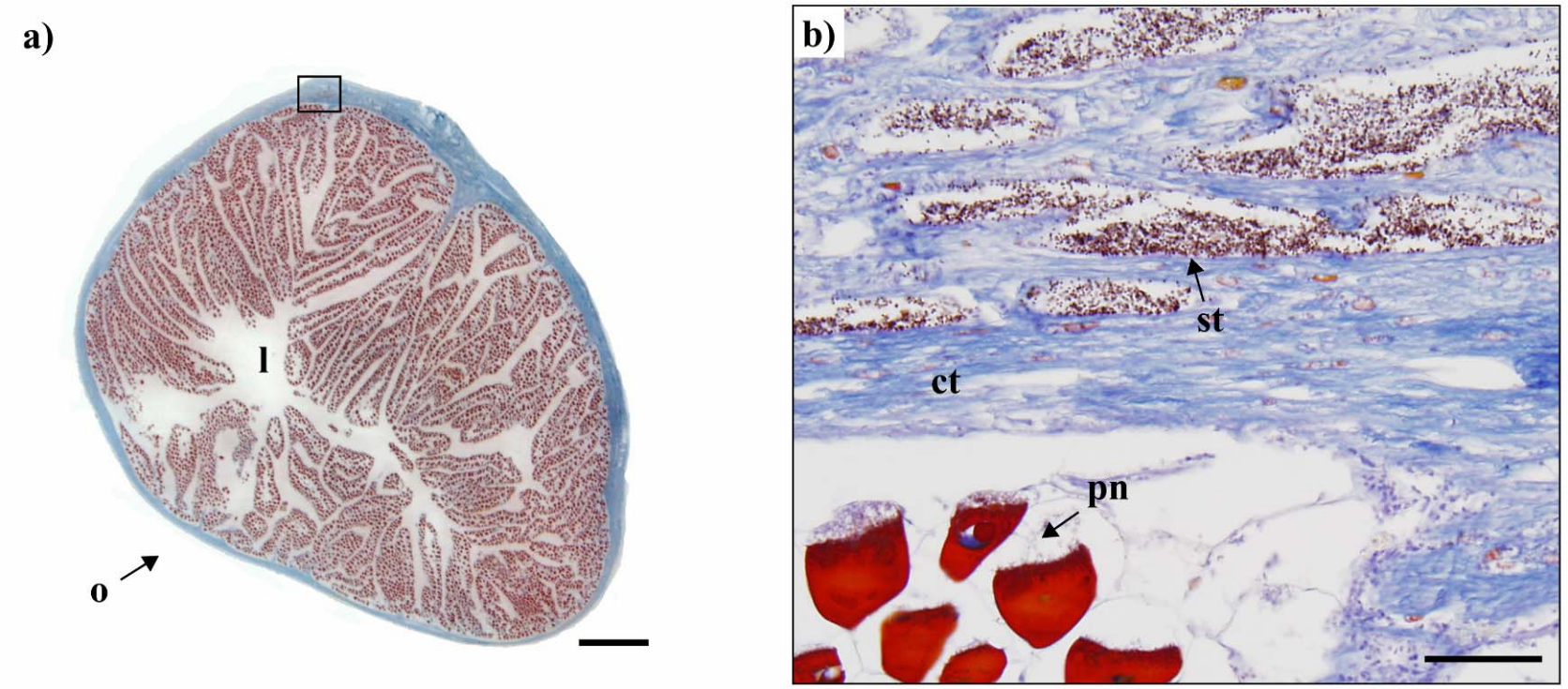

Plate 5.8. a) Low power and b) high power photographs of transverse section through the mid-region of a bisexual gonad from *Polydactylus macrochir* (526 mm TL), which comprises predominantly ovarian tissue. ct, connective tissue; l, ovarian lumen; o, ovary; pn, perinucleolar oocyte; st, spermatid; Scale bars in (a) & (b) represent 1 mm and 50 µm, respectively..

5.3.3. Pathway for protandrous sex change

The length and age distributions of the males and females of *E. tetradactylum* described above (Chapter 5.2.1) show that all small and young fish were males and all larger and older fish were female. The disparity in the lengths and, more particularly, the ages of the males and females of *E. tetradactylum* provides overwhelming evidence that the females of *E. tetradactylum* are derived from their males and that this threadfin species is thus a protandrous sequential hermaphrodite in north-western Australia (see Discussion). This hypothesis is further supported by the fact that the length range of fish with bisexual gonads, *i.e.* with both testicular and ovarian tissue, spanned the length range between the upper end of that for males and the lower end of that for females. In contrast to *E. tetradactylum*, the lengths of male, female and bisexual *P. macrochir* were widely distributed and showed considerable overlap. However, all small and young fish were likewise males and the prevalence of females increased progressively with increasing length and age. Thus, it follows that *P. macrochir* is also a protandrous synchronous hermaphrodite in north-western Australia (see Discussion).

Further evidence of protandry in both *E. tetradactylum* and *P. macrochir* is provided by the fact that some of the bisexual gonads in each species clearly contained proliferating ovarian tissue in addition to degenerating testicular tissue (Chapter 5.3.2).

These bisexual individuals represent fish that are part-way through their transition from functional male (evidenced by spermatozoa in the testicular duct) to functional female and are subsequently referred to as transitional individuals. It thus follows that that the three categories of bisexual gonads outlined above, *i.e.* predominantly testis (≥ 2/3 testicular tissue), similar testicular and ovarian contributions (1/3 to 2/3 testicular tissue) and predominantly ovary (≤ 1/3 testicular tissue) represent three sequential stages in the protandrous change of these species and correspond to gonads in the early, middle and late stages of transition, respectively (**Plate 5.9**).

5.3.4. Timing of sex change

Fish with gonads containing both testicular and ovarian components, and which are thus assumed to be changing from male to female, are subsequently referred to as transitional

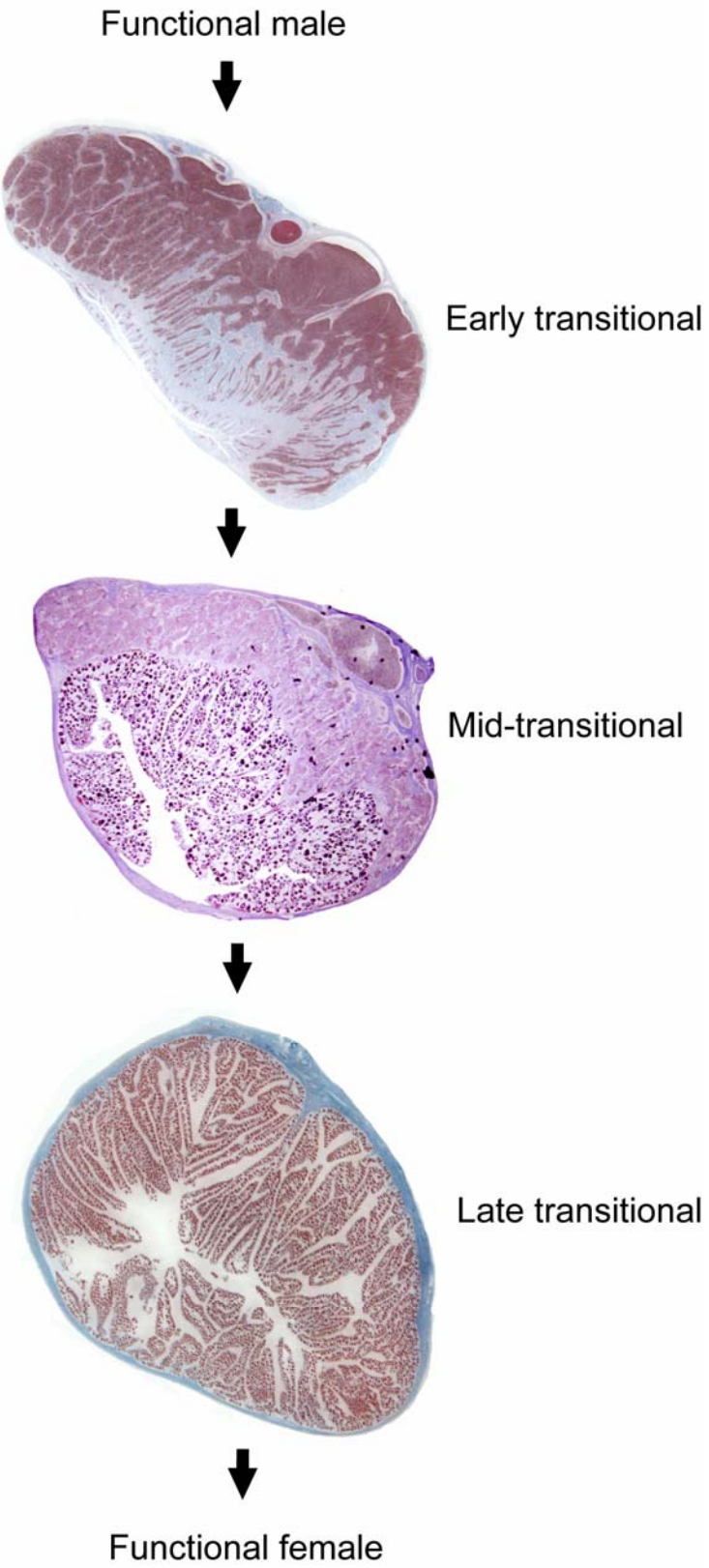

Plate 5.9. Proposed pathway for protandrous sex change from functional male to functional female for *Eleutheronema tetradactylum* and *Polydactylus macrochir*. Transverse sections of early, mid- and late transitional gonads are from *P. macrochir* measuring 437, 313 and 526 mm TL, respectively.

individuals. The high number of transitional *E. tetradactylum* collected during this study meant that the timing of sex change in that species could be investigated further. Note that it was not possible to conduct these analyses for *P. macrochir* due to the relatively small number of transitional individual collected.

Each monthly sample of *E. tetradactylum* always contained some transitional fish. The monthly contribution of these transitional fish to the total number of fish over the size range that sex change typically takes place (*i.e.* between 300 and 450 mm) fluctuated between *ca* 30 and 80% (**Figure 5.4**). The extent to which transitional *E. tetradactylum* had changed from male to female varied, with all three transitional categories, *i.e.* early, mid and late transitional, being represented in samples from seven months. However, the gonads of the majority of transitional *E. tetradactylum* in spring were in the early transitional phase, and thus the mean monthly testicular contribution to transitional gonads was elevated in these months, peaking at *ca* 80% in November when no late transitional fish were caught (**Figure 5.5**). The mean monthly contribution of testicular tissue declined during the summer months, when the majority of transitional fish belonged to the mid-transitional category (**Figure 5.5**).

The mean monthly GSIs for the testicular component of transitional gonads of *E. tetradactylum* underwent pronounced seasonal changes, rising from < 0.4 in June to August to > 1.5 in September to November and then declining to 0.8 in December and < 0.3 in January and subsequent months (**Figure 5.6**). In contrast, the mean monthly GSIs for the ovarian component of transitional gonads did not undergo a pronounced seasonal change and was always < 0.5 (**Figure 5.6**).

5.3.5. Size and age at sex change

A preliminary examination suggested that the distributions of the lengths of males, transitional individuals and females of *E. tetradactylum* did not differ conspicuously among the four sampling regions, *i.e*. Roebuck Bay, Anna Plains, Eighty Mile Beach and Cape Keraudren (**Figure 5.7**). The logistic regression analysis describing the relationship between the total length and probability that an individual has completed the change from male to female (*i.e.* is female) at Roebuck Bay, Anna Plains, Eighty Mile Beach and Cape

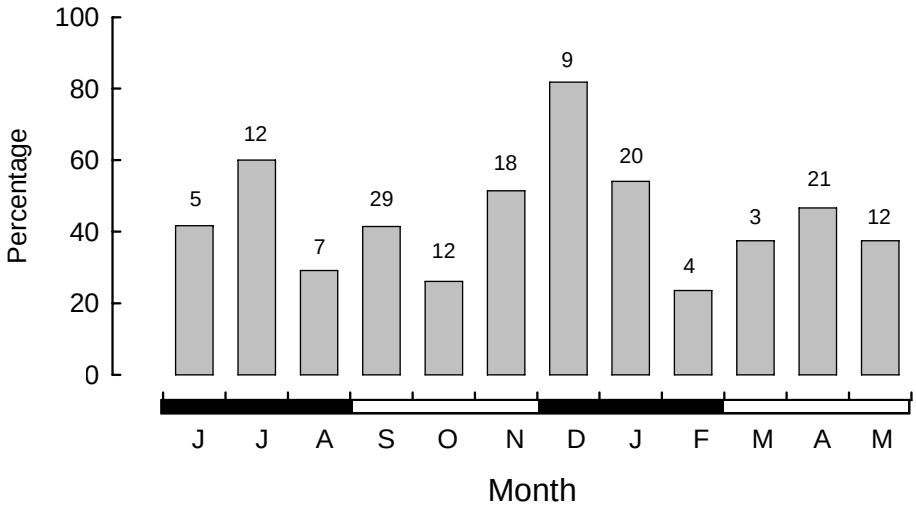

Figure 5.4. Monthly percentage contributions of transitional fish to the total number of *Eleutheronema tetradactylum* in the length range of 300 and 450 mm, which encompasses virtually all transitional *E. tetradactylum* (see Figure 5.2). Numbers above monthly bars denote the number of transitional *E. tetradactylum*. In this and following figures, closed rectangles on the horizontal axis refer to winter and summer months and open rectangles to spring and autumn months.

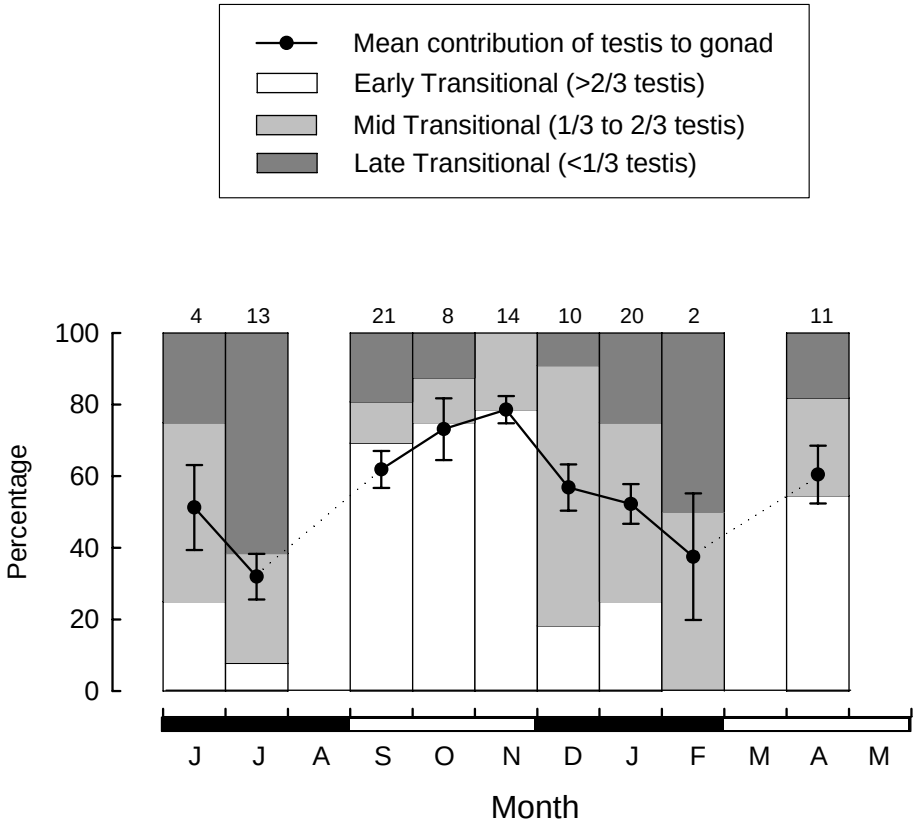

Figure 5.5. Mean monthly contribution of testicular tissue to transitional gonads of *Eleutheronema tetradactylum* (closed circles ±1SE) and the monthly proportions of the different transitional gonad categories of *E. tetradactylum*. White bars = early transitional (predominantly testis), light grey = mid transitional (similar testicular and ovarian contributions) and dark grey = late transitional (predominantly ovary) Numbers above monthly bars indicate the numbers of transitional fish used for estimating the proportions of their testis and ovary. Note that the numbers in each month differ from the previous figure as it was not possible to estimate ovarian/testicular proportions for all transitional fish and although transitional fish were collected in each month, proportions were not estimated for any *E. tetradactylum* during the months of March, May and August.

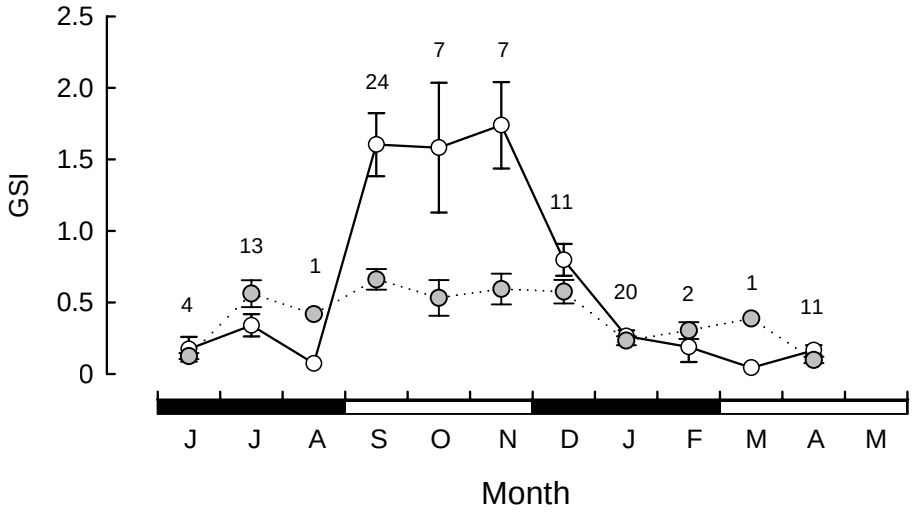

Figure 5.6. Mean monthly GSIs (±1SE) for the testicular (open circles) and ovarian (closed circles) components of the gonads of transitional individuals of *Eleutheronema tetradactylum*. Numbers above points are sample sizes for each month.

Keraudren yielded L_{50}s of *ca* 388, 369, 406 and 364 mm, respectively (**Table 5.3**, **Figure 5.7**). Although likelihood-ratio tests suggested that the L_{50} at Eighty Mile Beach was greater than at Roebuck Bay and Cape Keraudren (**Table 5.4**), this may represent an artefact produced by large sample sizes of fish in the length range over at which sex change occurs at the former region. Thus, the length data for each of the above three categories of fish from each region were pooled, which had the advantage of ensuring that there were a substantial number of fish represented in each of the 25 mm length classes that spanned the lengths at which sex change occurred.

The logistic regression analysis describing the relationship between the total length and probability that an *E. tetradactylum* individual is female or transitional between male and female derived from logistic regression analysis, yielded a L_{50} of 325 mm (**Table 5.5, Figure 5.8**). This corresponds to the length at which 50 % of *E. tetradactylum* have commenced their change from male to female. A logistic curve relating the proportions of just females at each length to their length yielded a L_{50} of 397 mm, which corresponds to the length at which 50% of *E. tetradactylum* have completed their change from male to female (**Table 5.5, Figure 5.8**). All *E. tetradactylum* in their first year of life were males

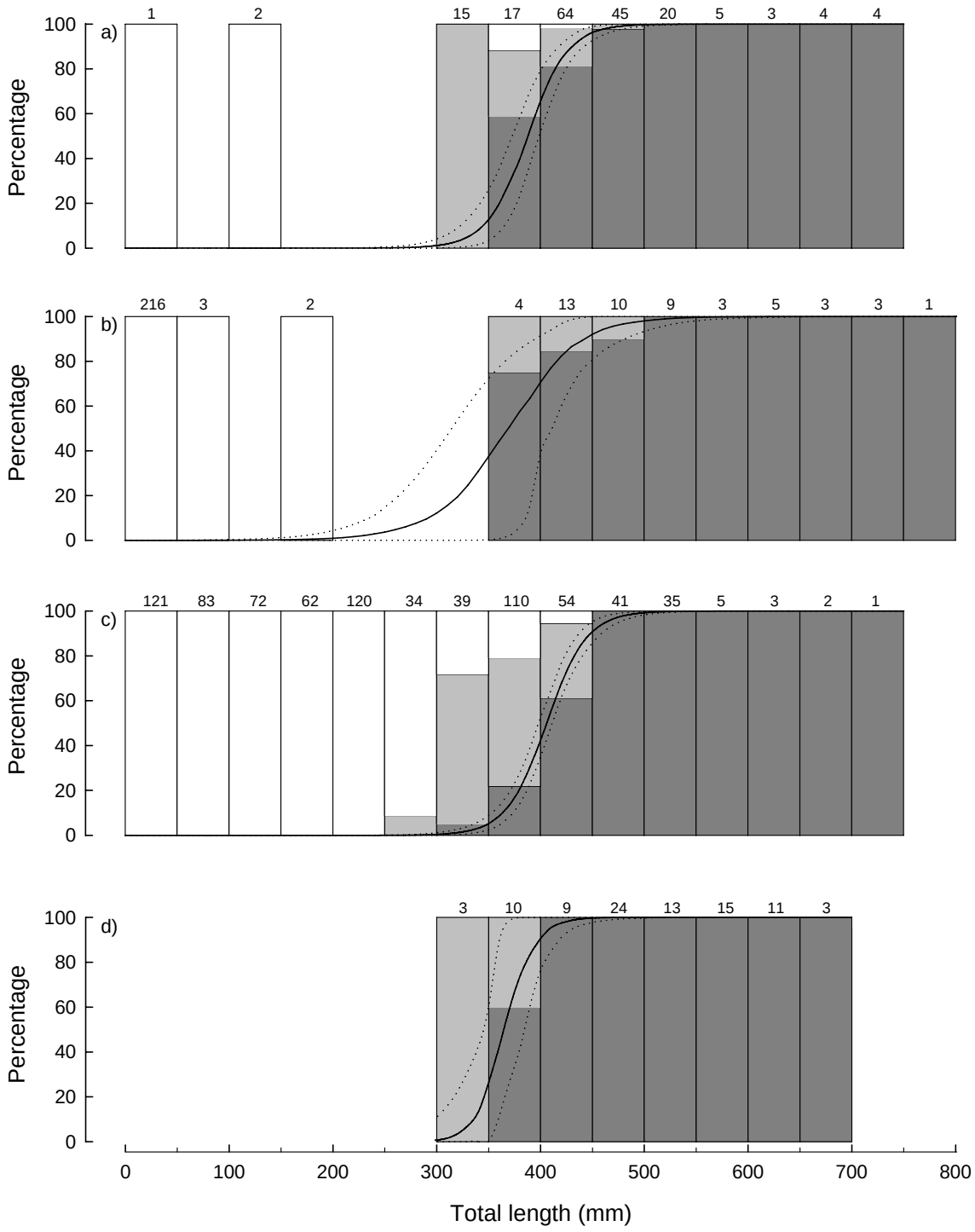

Figure 5.7. Frequencies of male (white), transitional (light grey) and female (dark grey) *Eleutheronema tetradactylum* in each 50 mm length class in samples from nearshore waters at a) Roebuck Bay, b) Anna Plains, c) Eighty Mile Beach and d) Cape Keraudren. The logistic curves (solid line) and their associated 95% confidence limits (dotted lines) were derived from logistic regression analysis that described the relationship between total length and probability that an individual had completed its change from male to female. The resultant L_{50}s thus represent the values for the completion of sex change at each region (see Table 5.3). Numbers above bars are sample sizes for each length class.

Table 5.3. L_{50}s and L_{95}s (±95%CI) for *Eleutheronema tetradactylum*, at each region, derived from the logistic regression analysis describing the relationship between the total length and probability that an individual has completed the change from male to female.

Region	Total length at sex change (mm)					
	L_{50}	Lower 95% CI	Upper 95% CI	L_{95}	Lower 95% CI	Upper 95% CI
Roebuck Bay	388	373	399	445	431	460
Anna Plains	369	315	411	466	415	513
Eighty Mile Beach	406	398	412	463	449	476
Cape Keraudren	364	346	384	409	363	431

Table 5.4. Significance of likelihood ratio tests of logistic models of the lengths at sex change for *Eleutheronema tetradactylum* at Roebuck Bay, Anna Plains, Eighty Mile Beach and Cape Keraudren. C, L_{50}, and L_{95}, denote that the logistic curves, the L_{50}s and/or the L_{95}s differ significantly ($p < 0.05$) between a region pair. ns = not significant.

	Length at sex change		
	Anna Plains	Eighty Mile Beach	Cape Keraudren
Roebuck Bay	ns	C, L_{50}	ns
Anna Plains	-----	ns	ns
Eighty Mile Beach	-----	-----	C, L_{50}, L_{95}

Table 5.5. L_{50}s and L_{95}s (±95%CI) for *Eleutheronema tetradactylum* derived from the logistic regression analysis describing the relationship between the total length and probability that an individual (pooled regions) has commenced or completed the change from male to female.

Pooled regions	Total length at sex change (mm)					
	L_{50}	Lower 95% CI	Upper 95% CI	L_{95}	Lower 95% CI	Upper 95% CI
Commencement of sex change	325	316	333	403	387	417
Completion of sex change	397	391	403	451	441	461

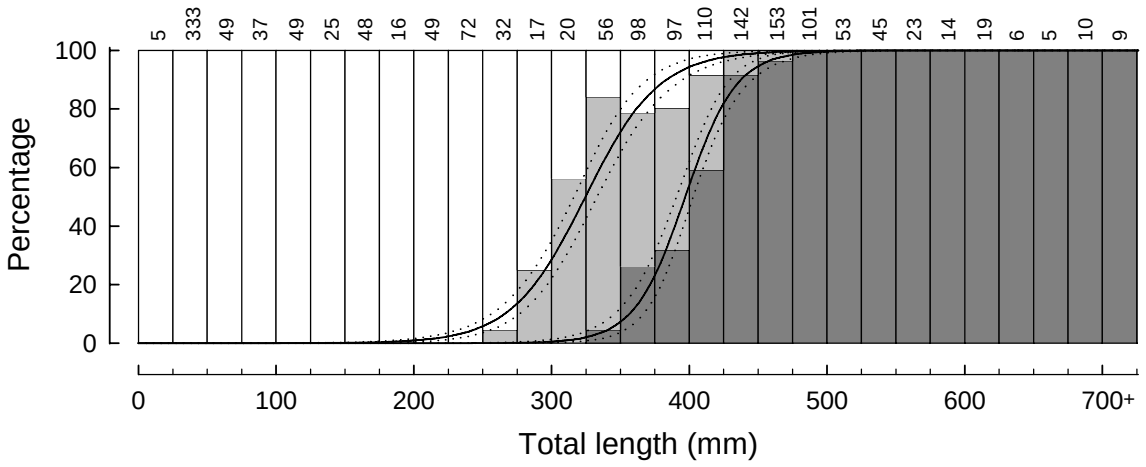

Figure 5.8. Frequencies of male (white), transitional (light grey) and female (dark grey) *Eleutheronema tetradactylum* in each 25 mm length class in samples obtained from nearshore waters in north-western Australia. The logistic curves (solid line) and their associated 95% confidence limits (dotted lines) were derived from logistic regression analyses that described the relationships between total length and the probability that an individual was, in the case of the first curve, either transitional or female, and, in the case of the second curve, just female. The resultant L_{50}s correspond to the L_{50} for the commencement and completion of sex change, respectively (see Table 5.5). Numbers above bars are sample sizes for each 25 mm length class.

and virtually all of those in their fourth and subsequent years of life were females (**Figure 5.9**). Fish in their second and third years of life contained males, females and transitional individuals, with the percentage of males declining from 85.3 to 12.1% and that of females increasing from 3.1 to 47.1% between the second and third years of life (**Figure 5.9**). The logistic regression analysis describing the relationships, for *E. tetradactylum*, between age and the probability that an individual has commenced or completed their change from male to female yielded A_{50}s of 1.46 and 2.00 years, respectively (**Table 5.6, Figure 5.9**).

During the spawning season (Chapter 5.3.7), those 1+ *E. tetradactylum*, *i.e.* fish at the end of their first year of life / beginning of their second year of life, were mature were almost exclusively males. The lengths of two other 1+ fish, which had transitional gonads, lay at the upper end of that of the age class. Fish from the 2+ age class collected during the spawning season were predominately females (43.4%) or transitional fish (41.4%), with the mean length of females (416 mm) being longer than those of both males (384 mm) and transitional fish (388 mm) (**Figure 5.10**). The 3+ contributors to spawning were almost exclusively females with only one male and three transitional fish caught. The lengths of these four individuals were less than those of the majority of females making up the remainder of the 3+ and subsequent cohorts. (**Figure 5.10**).

All but three of the 541 *P. macrochir* < 400 mm collected were males and all of those > 1200 mm were females. Furthermore, at all four regions, *i.e*. Derby, Roebuck Bay, Anna Plains and Eighty Mile Beach, the contribution of males to each size class decreased with increasing length, and that of females therefore increased (**Figure 5.11**). However, unlike the situation with *E. tetradactylum*, the precise length range over which *P. macrochir* changed sex differed considerably among the four sampling regions as is illustrated by the large range observed in the L_{50}s corresponding to the completion of sex change derived for each region, *i.e. ca* 793, 981, 1158 and 820 mm at Derby, Roebuck Bay, Anna Plains and Eighty Mile Beach, respectively (**Table 5.7**). Likelihood-ratio tests demonstrated that the L_{50} values calculated for each region were significantly different from one another except for the two most latitudinally separated regions sampled, *i.e.* Derby and Eighty Mile Beach (**Table 5.8**).

Table 5.6. A_{50}s and A_{95}s (±95%CI) for *Eleutheronema tetradactylum* derived from the logistic regression analysis describing the relationship between age and the probability that an individual (pooled regions) has commenced or completed the change from male to female.

Pooled regions	Age at sex change (years)					
	A_{50}	Lower 95% CI	Upper 95% CI	A_{95}	Lower 95% CI	Upper 95% CI
Commencement of sex change	1.46	1.40	1.53	2.09	1.95	2.22
Completion of sex change	2.00	1.93	2.07	2.77	2.65	2.90

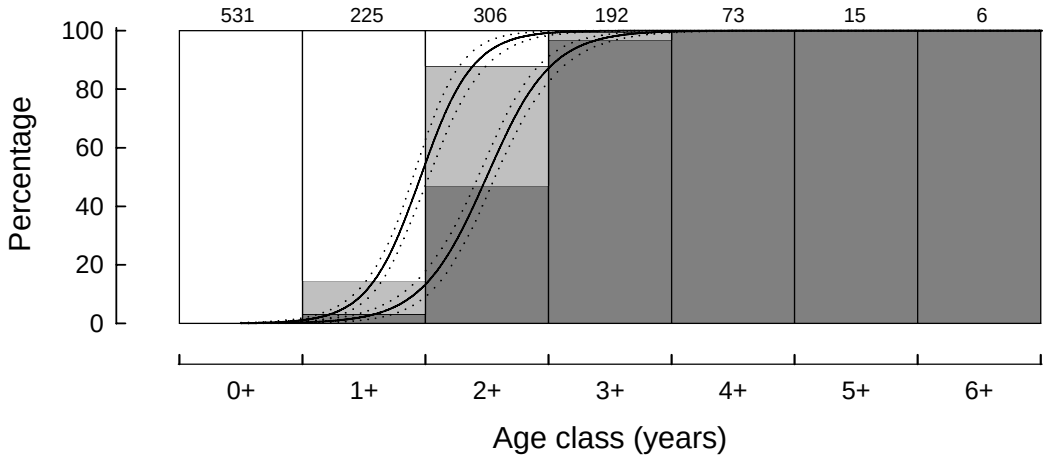

Figure 5.9. Frequencies of male (white), transitional (light grey) and female (dark grey) *Eleutheronema tetradactylum* in each age class in samples from nearshore waters in north-western Australia. The logistic curves (solid line) and their associated 95% confidence limits (dotted lines) were derived from logistic regression analyses that described the relationships between age and the probability that an individual was, in the case of the first curve, either transitional or female, and, in the case of the second curve, just female. The resultant A_{50}s corresponding to the A_{50} for the commencement and completion of sex change, respectively (see Table 5.6). Numbers above bars are sample sizes for each age class.

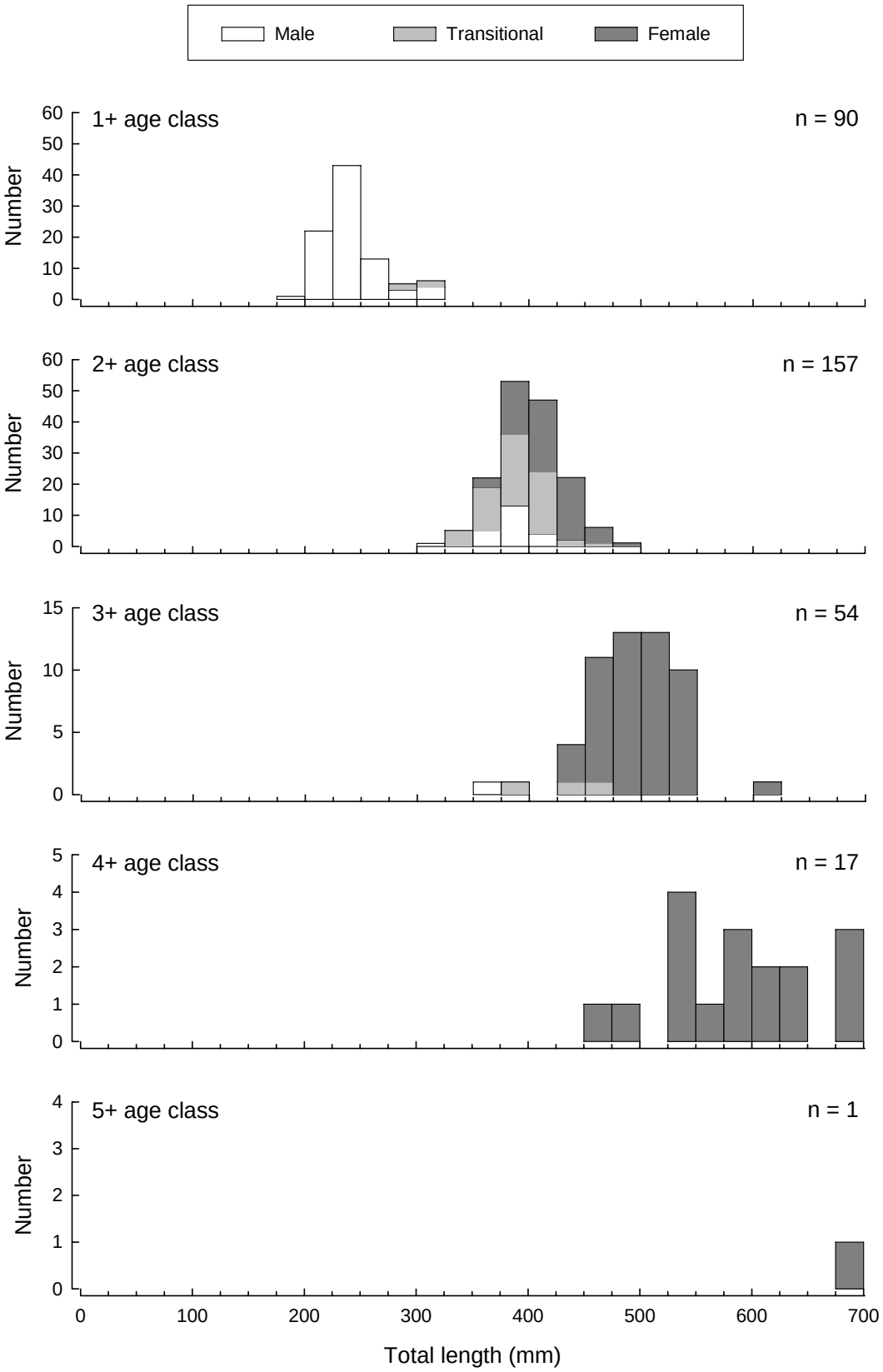

Figure 5.10. Contributions of male (white), transitional (light grey) and female (dark grey) *Eleutheronema tetradactylum* to each age class in samples collected, during the spawning period of this species, in nearshore waters in north-western Australia. Note that the few 1+ fish with gonads at stages < III, and which were thus considered unlikely to reach maturity within the spawning season, have not been included.

Table 5.7. L_{50}s and L_{95}s (±95%CI) for *Polydactylus macrochir* derived from the logistic regression analysis describing the relationship, at each region, between the total length and probability that an individual has completed the change from male to female.

Region	Total length at sex change (mm)					
	L_{50}	Lower 95% CI	Upper 95% CI	L_{95}	Lower 95% CI	Upper 95% CI
Derby	793	739	869	1101	977	1254
Roebuck Bay	981	954	1028	1123	1027	1240
Anna Plains	1158	1116	1224	1486	1396	1634
Eighty Mile Beach	820	749	909	1204	1052	1367

Table 5.8. Significance of likelihood ratio tests of logistic models of a) the lengths at sex change and b) the ages at sex change for *Polydactylus macrochir* at Derby, Roebuck Bay, Anna Plains and Eighty Mile Beach. C, L/A_{50}, and L/A_{95}, denote that the logistic curves, the L/A_{50}s and/or the L/A_{95}s differ significantly ($p < 0.05$) between a region pair. ns = not significant.

	a) Length at sex change			b) Age at sex change		
	Derby	Roebuck	Anna Plains	Derby	Roebuck	Anna Plains
Roebuck Bay	C, L_{50}	-----	-----	C, A_{50}	-----	-----
Anna Plains	C, L_{50}, L_{95}	C, L_{50}, L_{95}	-----	C, A_{50}, A_{95}	C, A_{50}, A_{95}	-----
Eighty Mile Beach	ns	C, L_{50}	C, L_{50}, L_{95}	ns	C	C, A_{50}, A_{95}

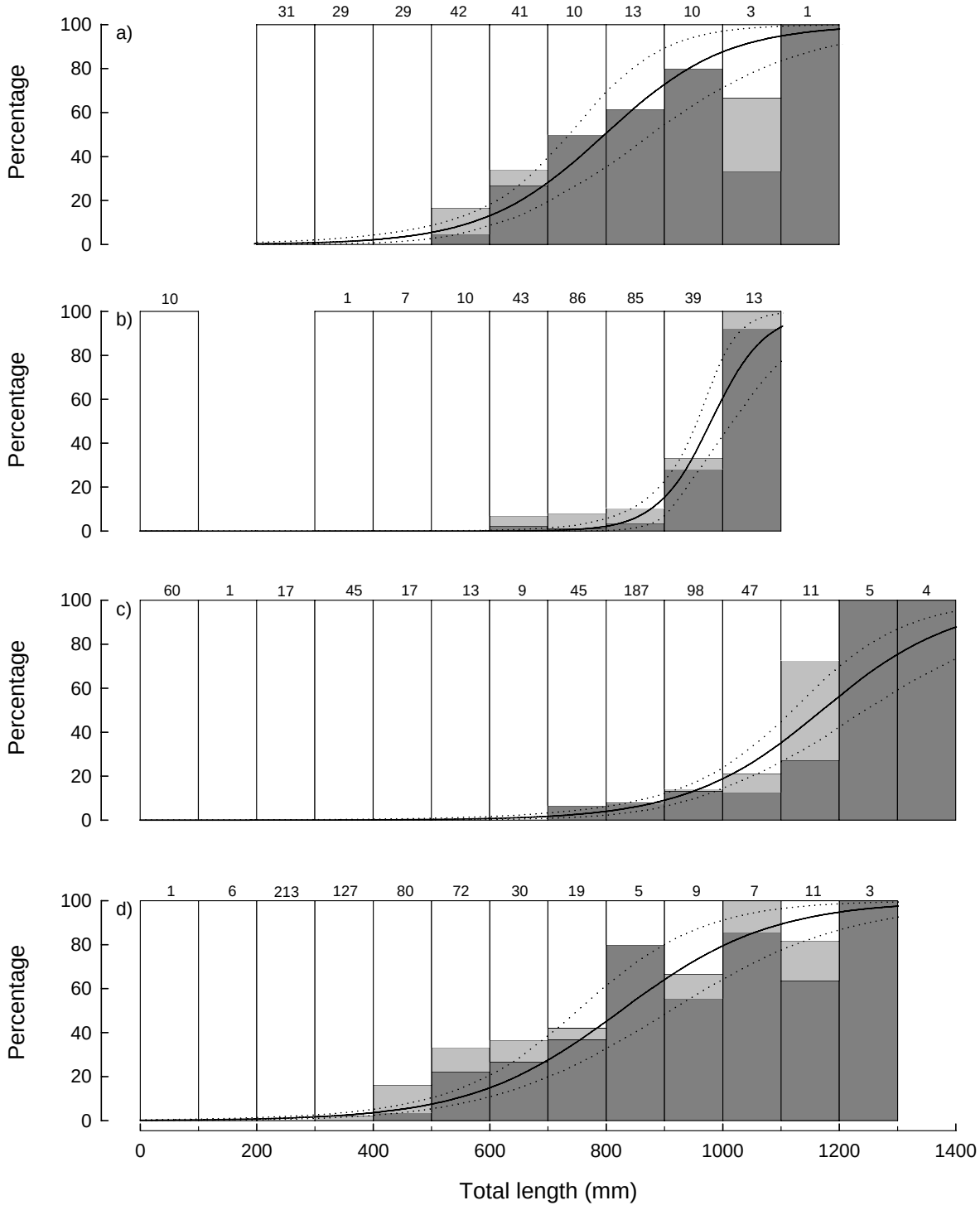

Figure 5.11. Frequencies of male (white), transitional (light grey) and female (dark grey) *Polydactylus macrochir* in each 100 mm length class in samples from nearshore waters at a) Derby, b) Roebuck Bay, c) Anna Plains and d) Eighty Mile Beach. The logistic curve (solid line) and its 95% confidence limits (dotted lines) are derived from a logistic regression analysis that described the relationship between total length and probability that an individual had completed sex change to become a female. The resultant L_{50}s correspond to the completion of sex change at each region (see Table 5.4). Numbers above bars are sample sizes for each length class.

All 0+ and virtually all 1+ *P. macrochir* were males and the percentage contributions of males decreased progressively at each region, such that at Derby and Anna Plains, the oldest males collected were 7+ individuals (**Figure 5.12**). Females first appeared in the 2+ age classes at Roebuck Bay and Eighty Mile Beach, the 3+ age class at Derby and the 4+ age class at Anna Plains. At each region, the proportion of females in each age class increased progressively with age and all fish in the 8+ and subsequent age classes were female (**Figure 5.12**). Small numbers of transitional fish were found in each age class between 1+ and 7+ (**Figure 5.12**). The A_{50} for sex change at Anna Plains of 6.73 y was significantly greater than that in each other region. Furthermore, the A_{50} for sex change of 5.03 y at Roebuck Bay was significantly greater than that of 4.30 y at Derby but not that of 4.57 y at Eighty Mile Beach (**Table 5.8; 5.9**).

Table 5.9. A_{50}s and A_{95}s (±95%CI) for *Polydactylus macrochir* derived from the logistic regression analysis describing the relationship, at each region, between the age and probability that an individual has completed the change from male to female.

Region	Age at sex change (years)					
	A_{50}	Lower 95% CI	Upper 95% CI	A_{95}	Lower 95% CI	Upper 95% CI
Derby	4.3	3.9	4.9	6.5	5.4	7.9
Roebuck Bay	5.0	4.7	5.5	6.5	6.0	7.7
Anna Plains	6.7	6.3	7.2	9.3	8.5	10.3
Eighty Mile Beach	4.6	4.1	5.2	7.4	6.5	8.7

5.3.6. Size and age at maturity of males

During the spawning period, all males of *E. tetradactylum* < 196 mm were immature, whereas all of those > 249 mm were mature (**Figure 5.13**). The L_{50} for length at maturity was 201 mm (**Table 5.10**). All males of *P. macrochir* < 202 mm were immature and all of those > 412 mm were mature and the L_{50} for maturity was 229 mm (**Table 5.10, Figure 5.14**). The majority of the males of *E. tetradactylum* (72.2%) and *P. macrochir* (84.2%) reached maturity at the end of their first year of life and all individuals of both species were mature at two years of age and older.

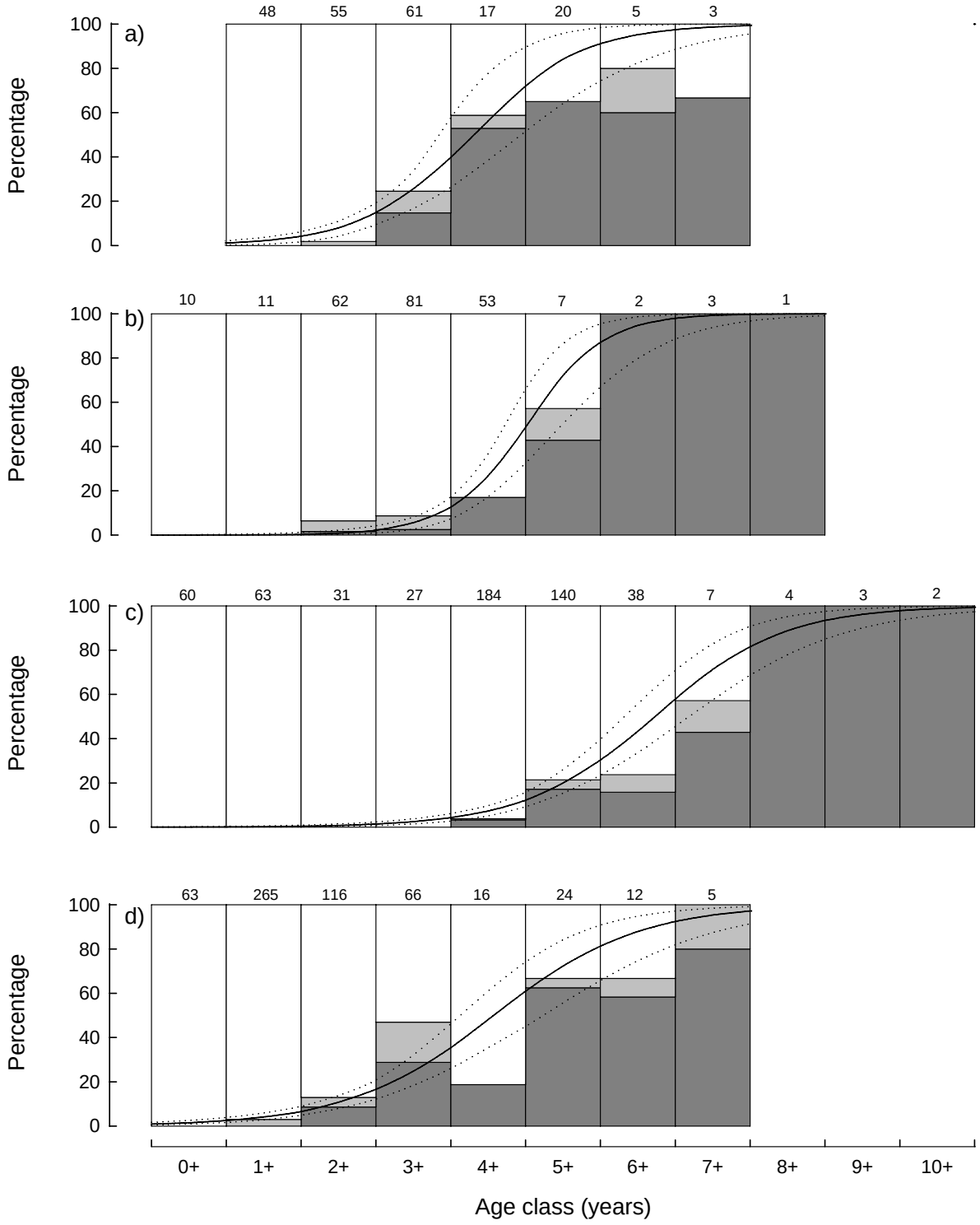

Figure 5.12. Frequencies of male (white), transitional (light grey) and female (dark grey) *Polydactylus macrochir* in each age class in samples from nearshore waters at a) Derby, b) Roebuck Bay, c) Anna Plains and d) Eighty Mile Beach. The logistic curve (solid line) and its 95% confidence limits (dotted lines) are derived from a logistic regression analysis that described the relationship between age and probability that an individual had completed sex change to become a female. The resultant A_{50}s correspond to the completion of sex change at each region (see Table 5.6). Numbers above bars are sample sizes for each age category.

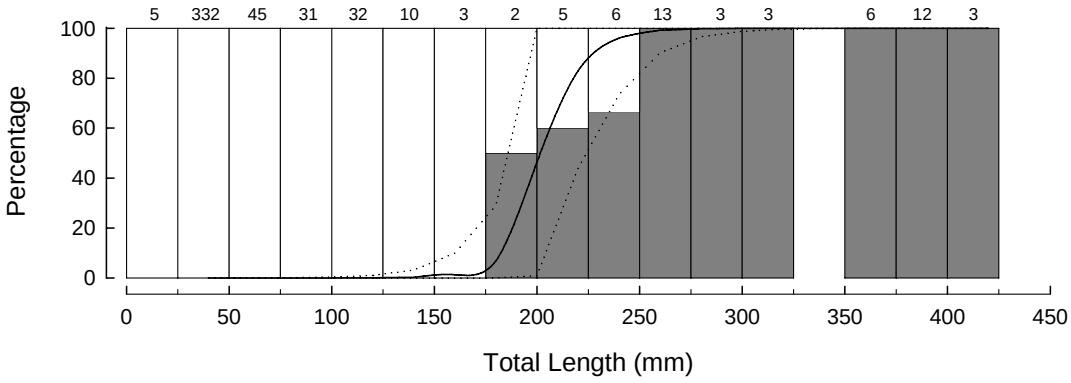

Figure 5.13. Percentage frequency of occurrence of immature (white) and mature (grey) males of *Eleutheronema tetradactylum* in each 25 mm length class during the spawning period. The logistic curve (solid line) and its 95% confidence limits (dotted lines) are derived from a logistic regression analysis that described the relationship between total length and the probability that an individual was mature. Numbers above bars are sample sizes for each length class.

Table 5.10. L_{50}s and L_{95}s (±95%CI) derived from the logistic regression analysis describing the relationship between the total length and probability that an individual male of *Eleutheronema tetradactylum* and *Polydactylus macrochir* is mature.

	Total length at first maturity (mm)					
Species	L_{50}	Lower 95% CI	Upper 95% CI	L_{95}	Lower 95% CI	Upper 95% CI
Eleutheronema tetradactylum	201.1	187.2	223.7	236.7	187.9	272.7
Polydactylus macrochir	229.0	210.9	247.2	354.4	323.0	384.9

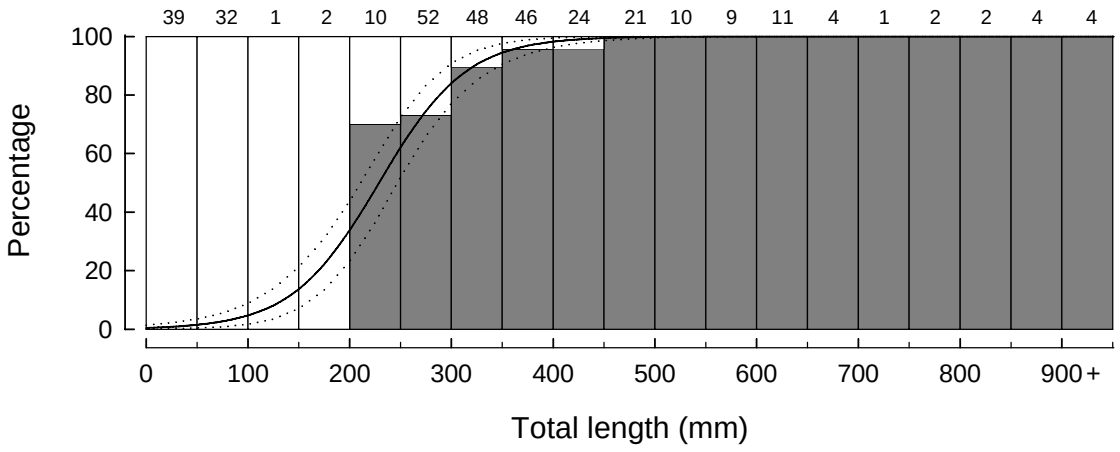

Figure 5.14. Percentage frequency of occurrence of immature (white) and mature (grey) males of *Polydactylus macrochir* in each 50 mm length class during the spawning period. The logistic curve (solid line) and its 95% confidence limits (dotted lines) are derived from a logistic regression analysis that described the relationship between total length and the probability that an individual was mature. Numbers above bars are sample sizes for each length class.

5.3.7. Timing and duration of spawning

The mean monthly gonadosomatic index (GSI) for male *E. tetradactylum* rose in an essentially progressive manner from 0.3 in June to 1.4 in August before declining markedly to 0.2 in January (**Figure 5.15a**). The mean monthly GSIs for transitional *E. tetradactylum* followed the seasonal trend as males, attaining a maximum of 2.7 in October (**Figure 5.15b**). Although there was a small decline in the mean monthly GSIs for female *E. tetradactylum* in October, the mean monthly GSIs otherwise showed a similar consistent seasonal trend, rising progressively through winter and reaching a maximum in spring, with values > 3 in September and November, and then declining sequentially during summer and early autumn (**Figure 5.15c**).

Resting ovaries (stage II) were found in some female *E. tetradactylum* in all months between January and August and was the only stage found in females sampled between March and June (**Figure 5.16**). Fish were first observed with developing gonads (stages III and IV) during July and, by the following month, such fish constituted *ca* 80% of all females. Females of *E. tetradactylum* with mature ovaries (stages V and VI) were found in small numbers in the latter month and were caught during the next five months, with their percentage contributions peaking at *ca* 85% in September and November. Fish

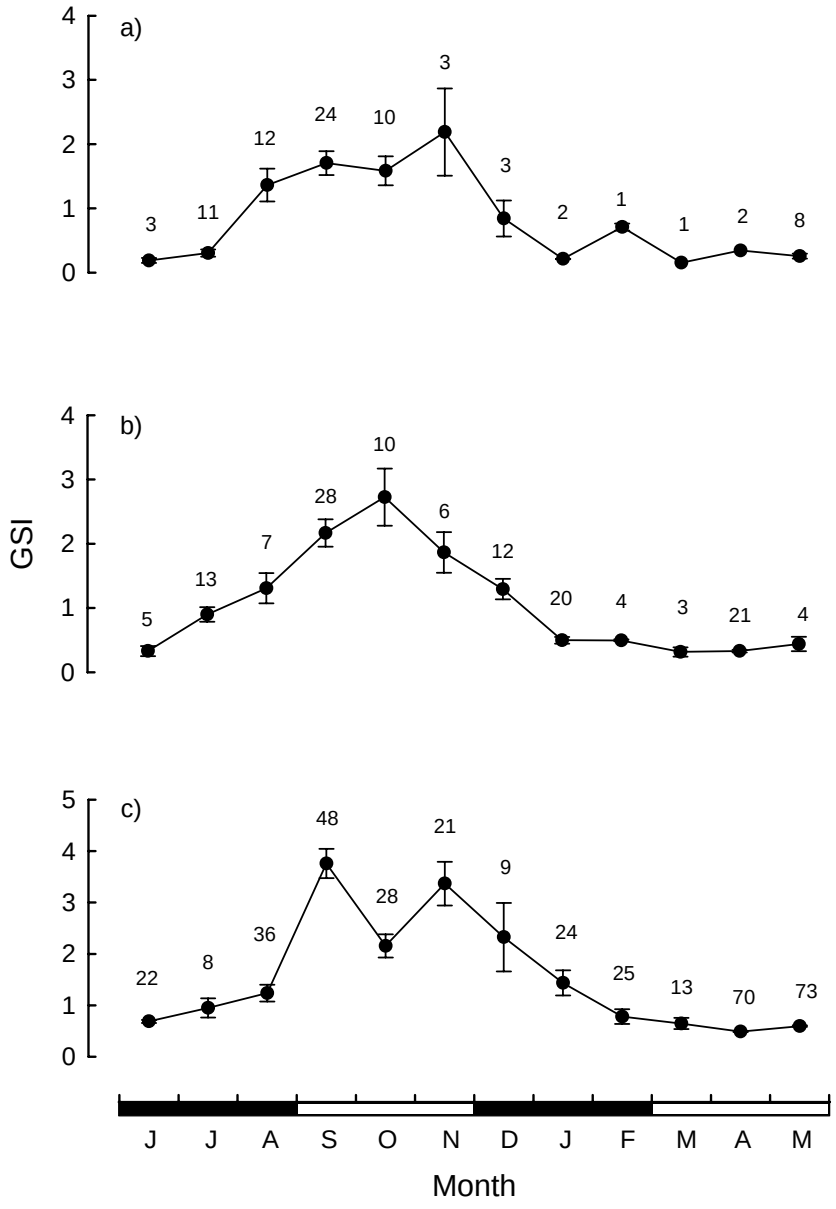

Figure 5.15. Mean monthly GSIs (±1SE) for a) male, b) transitional and c) female *Eleutheronema tetradactylum*. Data for males are derived from fish with lengths greater or equal to the length at 50% maturity.

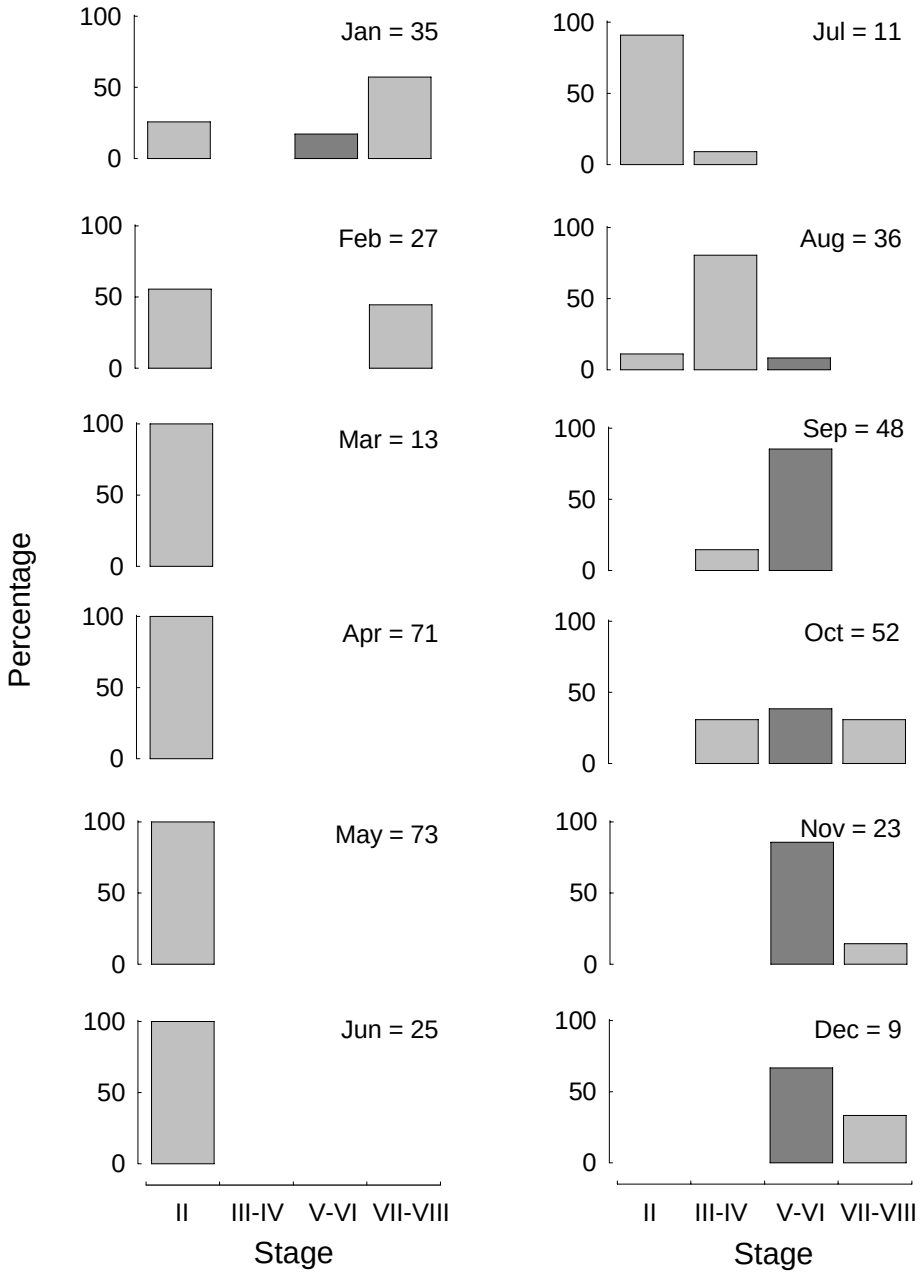

Figure 5.16. Monthly percentage frequencies of occurrence of sequential gonadal maturity stages in females of *Eleutheronema tetradactylum* in samples collected in nearshore waters in north-western Australia.

with spent and recovering ovaries (stages VII and VIII) were found between October and February. No mature individuals were recorded between February and July (**Figure 5.16**).

The ovaries of the two spawning (ovarian stage VI) females of *E. tetradactylum* examined both contained oocytes at each developmental stage between the chromatin nucleolar and yolk granule stage (**Figure 5.17**). The distributions of the oocyte diameters were virtually continuous in the first ovary, but formed two groups in the second ovary. This difference is due to the yolk granule oocytes having a larger size of in the second ovary, in which they produced a modal class at 375-399 mm. The distributions of the oocyte diameters for the chromatin nucleolar, perinucleolar and cortical alveolar oocytes in the two ovaries were very similar (**Figure 5.17a, b**).

The mean monthly gonadosomatic index (GSI) for male *P. macrochir* rose gradually from *ca* 0.1 in June and July to reach a maximum of *ca* 0.8 in October and then declined in the ensuing four months (**Figure 5.18a**). The mean monthly GSIs for transitional *P. macrochir* fluctuated little during the year, with their highest value of 0.5 being recorded in September (**Figure 5.18b**). The mean monthly GSIs for female *P. macrochir* rose from a low of 0.3 in August to high levels in October, December and January and then declined (**Figure 5.18c**). The mean weight of mature (Stage V-VI) testes increased progressively with the total length of males from a value of 1.1 g in the 0-250mm length class to a maximum of 29.0 g in the 1000-1250 mm class. In contrast, the mean GSI of males reached a maximum of *ca* 1.4 in the 250-499 mm length class and then declined to a minimum of *ca* 0.3 for the 1000-1250 mm class (**Figure 5.19**).

Female *P. macrochir* with resting ovaries (stage II) were present in most months, whereas those with developing ovaries (stages III and IV) were almost entirely restricted to July to October (**Figure 5.20**). Mature and spawning gonads (stages V and VI) were found in female *P. macrochir* caught during September and October, and females with spent ovaries were found in October to February (**Figure 5.20**).

The oocyte diameter distributions for the chromatin nucleolar, perinucleolar and cortical alveolar oocytes in the ovaries of two spawning (stage VI) *P. macrochir* were each similar to those of the ovaries of the two spawning females of *E. tetradactylum* (*cf* **Figures 5.17** and **5.21**). The oocyte diameters approached more closely a continuous distribution in the first of the two ovaries (**Figure 5.21a, b**).

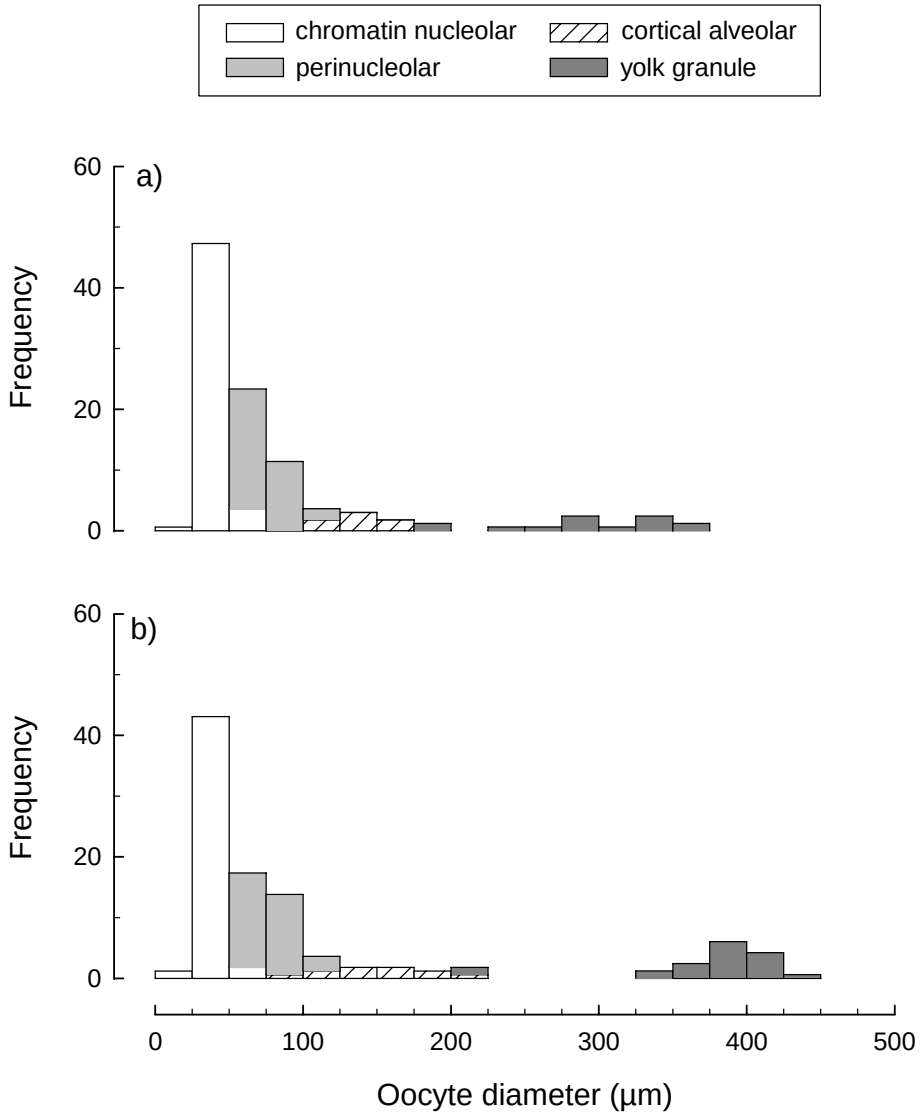

Figure 5.17. Frequency distributions for the diameters of oocytes in sequential developmental stages in histological sections of the ovaries of two spawning (stage VI) *Eleutheronema tetradactylum*. Ovaries were from a) a 598 mm fish caught in early December and b) a 400 mm fish caught in late October. Note that for this Figure and Figure 5.21 yolk granule oocytes with migratory nuclei and hydrated oocytes have not been included.

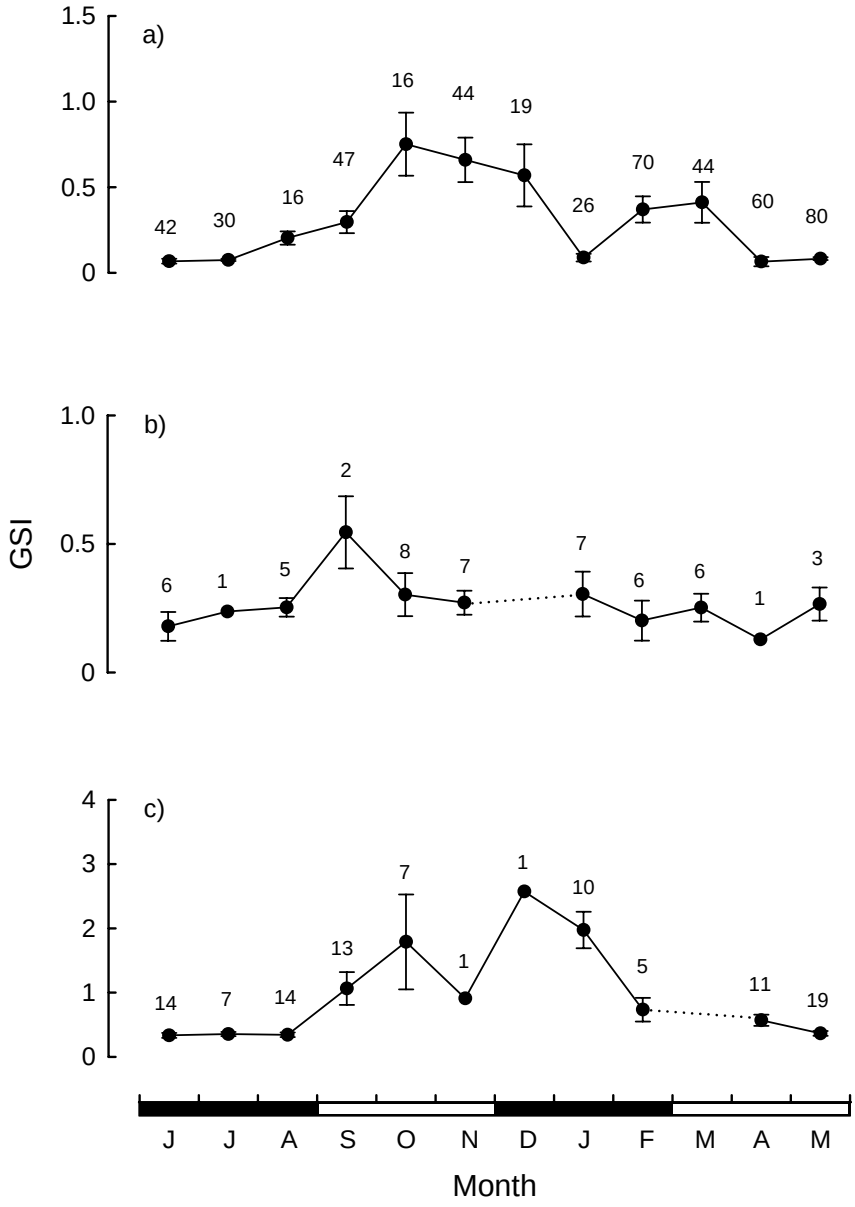

Figure 5.18. Mean monthly GSIs (±1SE) for a) male, b) transitional and c) female *Polydactylus macrochir* collected from nearshore waters. Data for males are derived from fish with lengths greater or equal to the length at 50% maturity.

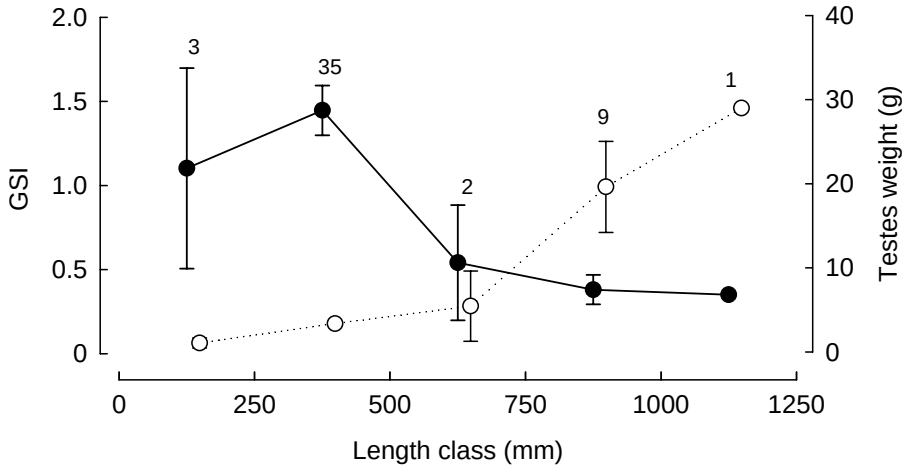

Figure 5.19. Mean weight (±1SE) (open circles) of testes and the corresponding mean GSIs (±1SE) (closed circles) derived for mature (Stage V-VI) male *Polydactylus macrochir* in each 250 mm length class. Numbers above points refer to sample sizes for each length class. Note that the same analyses were not performed for *Eleutheronema tetradactylum* as the males of that species display a much smaller length distribution.

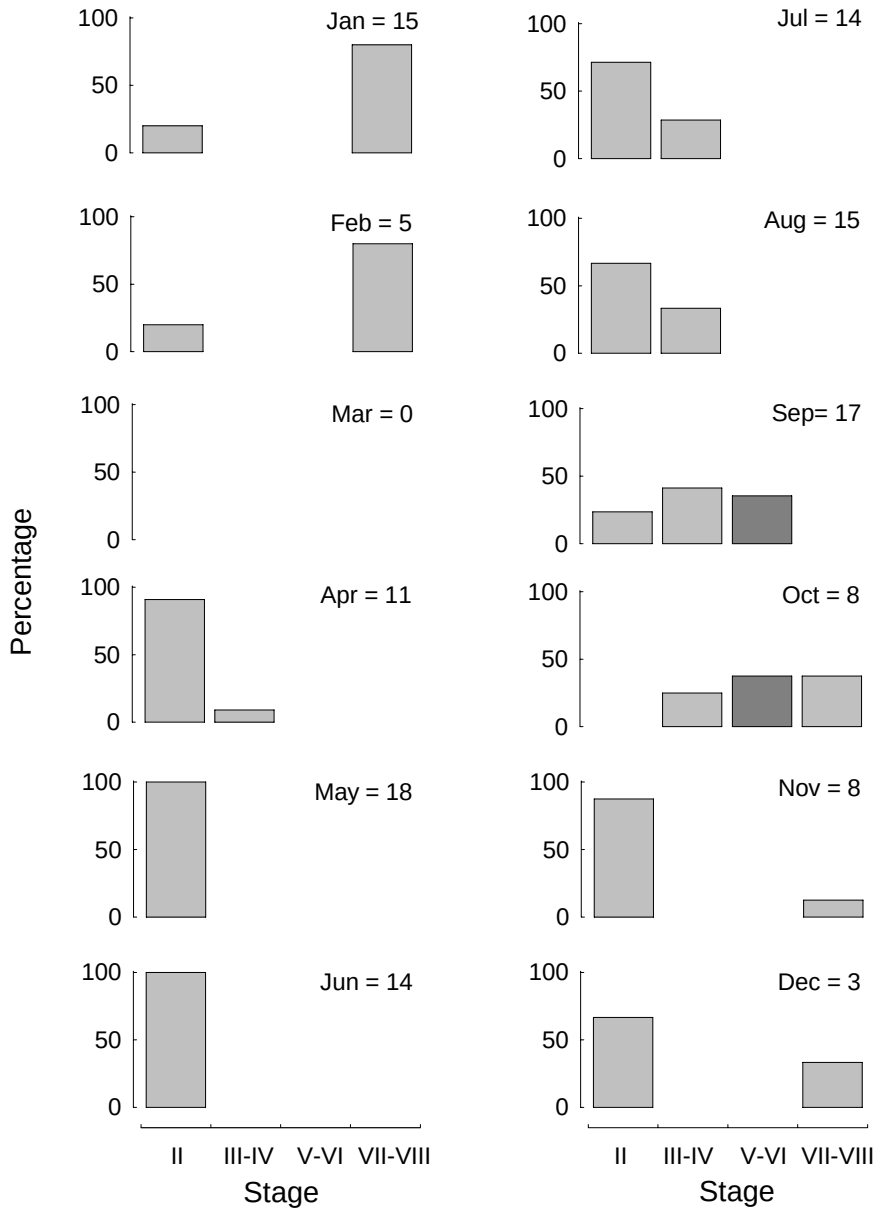

Figure 5.20. Percentage frequencies of occurrence of sequential gonadal maturity stages in females of *Polydactylus macrochir* in samples collected in nearshore waters in north-western Australia.

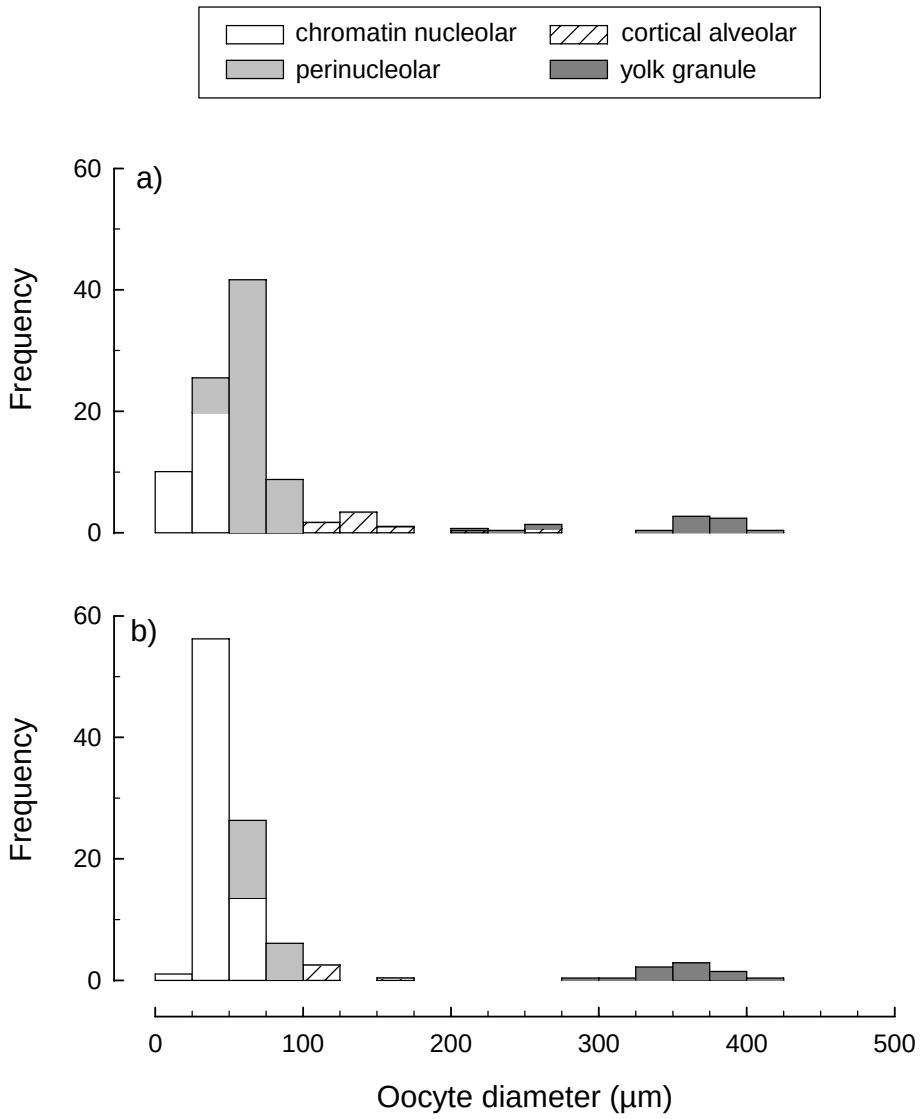

Figure 5.21. Frequency distributions for the diameters of oocytes in sequential developmental stages in histological sections of the ovaries of two spawning (stage VI) *Polydactylus macrochir*. Ovaries were from a) a 1339 mm fish and b) a 1155 mm fish caught in late October.

5.3.8. Habitats used by threadfin for spawning

During spring, when the 0+ age classes of both species are recruited into the shallows, a 21.5 m long seine net was employed to sample threadfin over fine substrate at Anna Plains and over sand at Eighty Mile Beach. The densities of *P. macrochir* but not of *E. tetradactylum*, derived from catches obtained using the above net, were significantly greater at Anna Plains than at Eighty Mile Beach ($p<0.05$) (**Figure 5.22**). However, at both locations, the densities of *E. tetradactylum* were markedly higher than those of *P. macrochir*. Although small meshed seine nets were also used to sample for threadfin over sand at Port Smith and Cape Keraudren, no new recruits of either *E. tetradactylum* or *P. macrochir* were collected at these two locations.

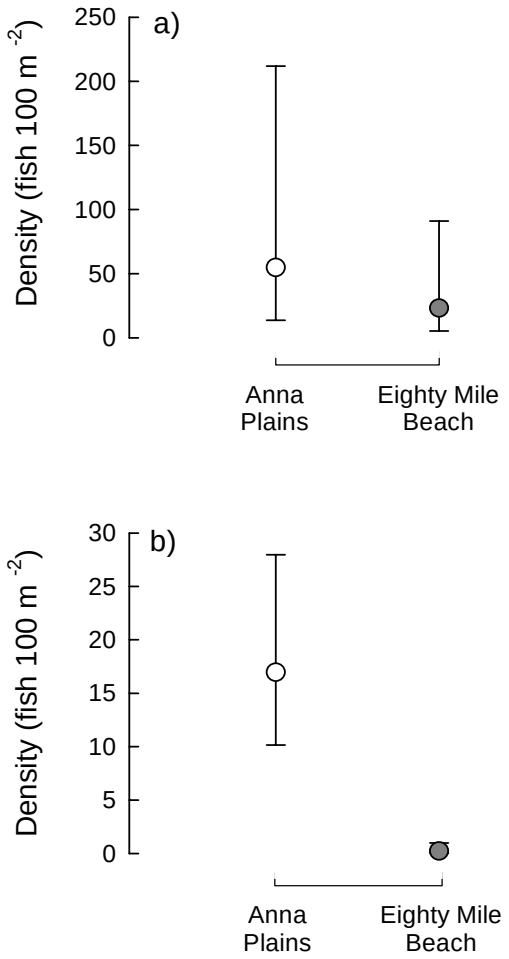

Figure 5.22. Mean densities ± 95 CL for a) *Eleutheronema tetradactylum* and b) *Polydactylus macrochir* derived from catches obtained with a 21.5 m seine net over silt at Anna Plains (open circles) and sand at Eighty Mile Beach (closed circles) during spring.

5.4. Discussion

5.4.1. Evidence that threadfin species are protandrous hermaphrodites

This study produced comprehensive data on the macroscopic and histological characteristics of the gonads of the Blue Threadfin *Eleutheronema tetradactylum* and King Threadfin *Polydactylus macrochir* in north-western Australia, based on a thorough examination of material from fish covering a wide range of lengths and ages and from all months of the year and a number of locations. The following aspects of these data, which are the same for both species, provide overwhelmingly support for the hypothesis that *E. tetradactylum* and *P. macrochir* are both protandrous hermaphrodites in north-western Australia, i) Length and age distributions for male and female threadfin are "bimodal". ii) The individuals with bisexual gonads lie in the upper end of the length range of males and lower end of the lower end of the length of females. iii) Many of the bisexual gonads of each of these species contained proliferating ovarian tissue and degenerating testicular tissue.

Bimodal length and age distributions of males and females

In the case of *E. tetradactylum,* all small and young fish were males and the prevalence of females increased markedly within a relatively narrow range in length and age. This point is illustrated by the fact that the lengths of males and females showed only a small amount of overlap and the 2+ age class was the only age class that contained substantial numbers of both sexes. Although the lengths and ages of the males and females of *P. macrochir* were widely distributed and both length and age showed considerable overlap between the sexes, all small and young individuals of this species were males. Furthermore, the prevalence of females of *P. macrochir* increased progressively with increasing length and age, with the result that, like *E. tetradactylum*, all older fish were female. The bimodality in the lengths of the males and females of *P. macrochir* became more apparent when the data for each region were analysed separately, reflecting the fact that the lengths and ages at which sex change occurs in this species vary among regions (see 5.4.2. below). The change from male to female with increasing size and age and the resultant bimodality in size and age distributions for the two sexes of the two species are characteristic of sequential hermaphroditism and resemble that described for other protandrous fishes

including clupeids (Blaber *et al*., 1999), creediids (Langston, 2004), eleginopids (Brickle *et al*., 2005) and other polynemids (Longurst, 1965; Hida, 1967).

Sadovy & Shapiro (1987) point out that a bias towards one sex in the samples of the smallest fish and youngest age classes may result from a sex specific differential use of habitats by young fish rather than sequential hermaphroditism. Such a scenario can essentially be ruled out for both *E. tetradactylum* and *P. macrochir* as the sampling regime encompassed a range of habitats and yielded small threadfin from each of those habitats in different areas and in all seasons. The lack of females in the smallest and youngest length and age classes of both threadfin species is thus presumably due to the males having not yet undergone a protandrous sex change. As sampling was conducted in different habitats in different areas and throughout the year, the fact that the larger and older individuals of *E. tetradactylum* and *P. macrochir* were females is very unlikely to have been due to a bias for females to occupy a particular habitat. The fact that all of those larger females were also older than any males also strongly supports the view that the bimodality in the length distributions for the two sexes cannot be attributed to a faster growth rate of females. It therefore provides a contrast with the situation in certain gonochroristic species in which bimodality in the length distributions of the males and females reflect differences in growth between the sexes. Examples of this phenomenon are found in the Lutjanidae (*e.g.* Grimes & Huntsman, 1980; Grimes, 1987), Clupeidae (Blaber *et al*., 2003) and Salmonidae (Olsen *et al*., 2006).

Length and age distribution of bisexual individuals

The fact that, in both species, the lengths and ages of the substantial number of those fish with bisexual gonads spanned the length and age ranges between the upper end of that for males and the lower end of that for females provides additional evidence that *E. tetradactylum* and *P. macrochir* are sequential hermaphrodites in north-western Australia. This feature was particularly marked in *E. tetradactylum* with essentially all bisexual fish being restricted to a 150 mm length range and belonging to the 1+ and 2+ age classes. In contrast, the lengths of *P. macrochir* with bisexual gonads ranged over more than 700 mm and were found in small numbers in all age classes from the 1+ to the 7+. The wide length and age distribution of transitional *P. macrochir* reflects the fact that

only a small proportion of males of this species initiate the transition to female in any one year (see 5.4.3. below).

The structure of the bisexual gonads of *E. tetradactylum* and *P. macrochir* were essentially the same in both species, with the testicular tissue being located along the dorsal and inner lateral regions of the paired gonads and being separated from the ovarian tissue on the ventral and outer regions of those lobes by connective tissue. These locations of the testicular and ovarian components and their separation by connective tissue correspond to the arrangement described for the bisexual gonads of *E. tetradactylum* elsewhere (Patnaik, 1967; Stanger, 1974) and of other polynemids (Nyak, 1959; Kagwade, 1970; Dorairaj, 1973). The similarities in the architecture of the bisexual gonads of *E. tetradactylum* and those of *Leptomelanosoma indicum* and *Polydactylus mullani* (referred to previously as *Polydactylus indicus* and *Polynemus heptadactylya*, respectively) led Kagwade (1970) to propose that polynemids were typically hermaphroditic. Longurst (1965) and Hida (1967) had earlier suggested that *Galeoides decadactylus, Polydactylus sextarius* and *Polydactylus mullani*, which they were studying, were specifically protandrous hermaphrodites.

Simultaneous occurrence of proliferating ovarian tissue and degenerating testicular tissue

Further compelling evidence of protandrous hermaphoritism in *E. tetradactylum* and *P. macrochir* was the observation that proliferating ovarian tissue and degenerating testicular tissue were present in some of the bisexual gonads of both of these species. Moreover, degenerating testicular tissue was most conspicuous in those gonads that comprised predominantly ovarian tissue and in which the testicular component was represented by only a narrow rim along the dorsal wall. In some of these gonads, the sperm stained very darkly and were thus presumably pyknotic and no longer functional (Lofts *et al*., 1968). In contrast, the testicular component of early and mid- transitional gonads typically contained the full range of spermatogenic stages and were thus probably functional.

Oogonia were particularly numerous around the precursor to the ovarian lumen in early transitional gonads and, although the oocytes in such gonads did not typically develop beyond the perinucleolar stage, their abundance in later transitional stages

clearly indicates that oogenesis occurs during the change from testis to ovary. Early transitional gonads were also typified by the development of blood vessels in the connective tissue surrounding the early stage oocytes. As sex change in both protandrous and protogynous fish has been shown to be mediated by a suite of hormones, many of which are produced in the pituitary gland and brain (*e.g.* Bass & Grober, 2001; Frisch, 2004; Gardner *et al*., 2005), this vascularisation presumably facilitates the transport of these hormones from the brain and pituitary to gonadal cells (Lone *et al*., 2001; Devlin & Nagahama, 2002). The transport of metabolic requirements to developing oocytes is also presumably aided by the vascularisation of gonadal tissue.

As the testicular tissue and the developing ovarian component of transitional gonads are completely delineated by connective tissue and this delineation persists throughout the transition from testis to ovary, the gonads of *E. tetradactylum* and *P. macrochir* are essentially totally reorganised during sex change. Thus, the "terminal" gonad, comprising entirely ovarian tissue, retains no histological evidence of its testicular ancestry, a characteristic of protandrous fish (Sadovy & Shapiro, 1987). In contrast, following sex change, the terminal gonads of secondary males of protogynous hermaphrodites typically retain histological evidence of their ovarian past, *i.e.* a luminal space within the testis (*e.g.* Young & Martin, 1982).

The bimodality in the length and particularly age distributions of males and females, derived from representative samples, and the presence of degenerating testicular and proliferating ovarian material in bisexual gonads satisfy the criteria of Sadovy & Shapiro, (1987) for demonstrating that *E. tetradactylum* and *P. macrochir* are sequential protandrous hermaphrodites. This is consistent with the conclusion drawn for these two polynemids in the Northern Territory and Queensland (Stanger, 1974; R. Griffin unpubl. data, cited in Kailola *et al*., 1993; McPherson, 1997) and a number of other polynemid species, (Longhurst, 1965; Hida, 1967; Santerre & May, 1977; Szyper *et al*., 1991). However, the finding that *E. tetradactylum* is a protandrous hermaphrodite in Australian waters contrasts with the situation in Indian waters, in which this species is typically gonochoristic (Patnaik, 1967, 1970; Gopalakrishnan, 1972).

The fact that the smallest females of *E. tetradactylum* and *P. macrochir*, *i.e.* 330 and 440 mm, respectively, were longer than the lengths at which 95% of the males of these

species attain sexual maturity, *i.e.* 237 and 335 mm, respectively, suggests that all females are derived from males and are therefore secondary females. Thus, as there is only one pathway in the development of the females of *E. tetradactylum* and *P. macrochir*, these species can be referred to as *monogynic* protandrous hermaphrodites. Monogyny appears to be the typical condition in protandrous fishes and is essentially analogous to monandry, a characteristic of many protogynous hermaprodites, such as tuskfish (Labridae), where all males in a population are secondary males, *i.e.* derived from functional females (see for example Fairclough, 2005). The diagnosis that *E. tetradactylum* and *P. macrochir* are monogynous parallels the situation in some other protandrous polynemids including *Polydactylus sextarius,* and *P. sexfilis* (Hida, 1967; Santerre & May, 1977; Szyper *et al*., 1991). However, it differs from the situation in *Galeoides decadactylus* which is digynic, *i.e.* contains secondary females which develop from functional males through sex change, and also primary females, which originate from undifferentiated juveniles (Longhurst, 1965).

5.4.2. Timing of maturation and sex change in Eleutheronema tetradactylum

The fact that the majority of *E. tetradactylum* reached maturity at the end of their first year of life when they were 200-300 mm in length and immediately contributed to spawning as males closely parallels the situation recorded for *E. tetradactylum* in Indian (Patnaik, 1970) and eastern Australian waters (Stanger, 1974). By the following and second spawning period, 43% of the individuals of *E. tetradactylum* had completed sex change and become mature females. As those females were the largest of the two year old individuals, the mechanisms in initiating sex change in *E. tetradactylum* include factors related to the attainment of a critical length.

Although a further 41% of two year old and generally smaller *E. tetradactylum* possessed gonads that had commenced the change from testis to ovary, those gonads still consisted predominantly of testicular material and were producing sperm and were thus presumably functional. This view is consistent with the fact that, during the spawning period, the GSIs for the male component of transitional fish rise to far greater levels than those of the female component and indeed were comparable with those of definitive

males. The apparent involvement of factor(s) related to the attainment of a particular narrow length range as a cue for sex change in *E. tetradactylum* differs from the situation in the majority of sequential hermaphrodites in which sex change occurs over a wide range of lengths and is influenced by proximate cues, *e.g.* the sex ratio of the mature stock (Ross, 1990; Vincent & Sadovy, 1998).

As all female *E. tetradactylum* become mature during the spawning period, the L_{50} for the completion of sex change essentially corresponds to the L_{50} of females at maturity. This L_{50}, *i.e.* 397 mm, is far lower than the *ca* 650 mm (543 mm FL) recorded for the L_{50} at maturity by McPherson (1997) for this species in the Gulf of Carpentaria. However, as pointed out by McPherson (1997), the logistic equation did not provide a good fit to the data for the latter region.

The L_{50} of 397 mm for sex change in *E. tetradactylum* corresponds to *ca* 50% of the maximum total length of 793 mm recorded for this species during this study (see Chapter 6). Thus, *E. tetradactylum* does not conform closely to the constant relative size at sex change theory for sequential hermaphroditic species, in which sex change is predicted to occur at lengths approximating to 72-80% of the maximum length of those species (Allsop & West, 2003a,b, 2004; Buston *et al*., 2004).

Stanger (1974) hypothesised that sex change in *E. tetradactylum* in eastern Queensland was initiated immediately after the spawning season and that the transition took at least a year. However, the view that the transition occupied a protracted period was based on a data derived from a sampling regime that did not include the spawning period. The results of the present study suggest that sex change in *E. tetradactylum* is competed within a far shorter period, *i.e. ca* six months. This conclusion is based on the fact that the difference between the A_{50}s at the commencement and completion of sex change, derived from logistic regression analysis of the prevalence of females at sequential lengths, is 0.54 years. This period of approximately six months provides the most concise estimate of the time required for any polynemid to complete sex change from male to female.

A period of a approximately six months for *E. tetradactylum* to complete sex change contrasts markedly with the situation observed in most protogynous species where the onset of sex change may be induced in an individual only hours after the loss of the male from the social group and is typically completed within days (*e.g.* Robertson, 1972;

Shapiro, 1981b) and consequently, transitional individuals are rarely observed (*e.g.* Crabtree & Bullock, 1998). The substantial time required by this protandrous threadfin species largely reflects the fact that, unlike the majority of protogynous species, the gonads undergo complete restructuring during sex change (Reinboth, 1988). Other protandrous species in which the gonads undergo substantial reorganisation during sex change, such as creediids, have been shown also to take a long period (*i.e* up to 30 months) to undertake the complete transition from male to female (Langston, 2004). Although sex change in protandrous centropomids is reported to be completed rapidly, the ovaries of this group still take a year to reach their definitive condition (Taylor *et al*., 2000). Moreover, while sex change in the protandrous anemonefish (Pomacentridae) is typically completed within six weeks (Godwin, 1994), the testicular and ovarian component of the gonads of this species are not delineated by connective tissue and have only to undergo a moderate degree of reorganisation compared with that described for *E. tetradactylum* during the present study (Brusle-Sicard & Reinboth, 1990). In addition, unlike the situation in *E. tetradactylum*, the gonads of the males of anemonefishes already contain an ovarian component (Shapiro, 1992).

5.4.3. Timing of maturation and sex change in Polydactylus macrochir

Although the maximum total length of 1393 mm recorded for *P. macrochir* greatly exceeds the corresponding value of 793 mm for *E. tetradactylum* (see Chapter 6), the vast majority of the former species, like those of *E. tetradactylum*, reach maturity at the end of their first year of life when their lengths typically range from 250 to 300 mm. The similarity in the lengths and ages of the two species at first maturity is surprising since, on the basis of data for a wide range of families, the length at maturity has been shown to be strongly correlated with asymptotic length (Beverton, 1992; Stamps *et al*., 1998; Froese & Binohlan, 2000). However, the development of maturity at an early age appears to be a characteristic of polynemid fishes, as a number of other threadfin species, including *Polynemus paradiseus*, *Polydactylus octonemus* and *Polydactylus sexfilis,* also attain maturity at the end of their first year of life (Dentzau & Chittenden, 1990; Szyper *et al*., 1991; Mukhopadhyay *et al*., 1995). In contrast, *Leptomelanosoma indicum,* the only other

polynemid that reaches a length and age comparable to *P. macrochir* (*i.e.* 1100 mm and 7 years) is regarded not to reach maturity until it is *ca* 3 years old and has attained a length of *ca* 800 mm (Karekar & Bal, 1960; Kagwade, 1973). However, *L. indicum* is said to be essentially gonochoristic, but with some individuals being hermaphroditic (Kagwade, 1970), and it is unclear whether the maturity data of Karekar & Bal (1960) refer to the maturity of males and females or to just females.

The finding that the males of *P. macrochir* in north-western Australia mature at the end of their first year of life and at total lengths of 250 to 300 mm differs from the results of other workers for this species. For example, Russell (1988) and McPherson (1997) found that male *P. macrochir* began to reach maturity at two years of age and *ca* 350-400 mm in eastern Queensland and the Gulf of Carpentaria, respectively. Although it had been earlier reported that, in the Gulf of Carpentaria, the males of this species do not reach maturity until they are *ca* four years old and 600 to 800 mm in length (Garrett 1992; N.T. Fisheries, unpublished data), these ages and lengths are almost certainly overestimates as they were derived from samples obtained from commercial fishers, who target larger fish.

The data on the prevalences of males and females in sequential age and length classes (**Figures 5.11, 5.12**) demonstrate that sex change can occur in fish as young as two years old and up to eight years old and at lengths between 313 and 1139 mm. This situation contrasts with that recorded for *E. tetradactylum* in which virtually all males had changed to females by the end of their third year of life and the lengths over which sex change occurred ranged only from 279 to 455 mm. Thus, factors associated with the attainment of a particular length do not apparently have the same influence on sex change in *P. macrochir* as in *E. tetradactylum.* Furthermore, unlike the situation with *E. tetradactylum*, the L_{50} at sex change varied markedly among the populations of *P. macrochir* in the different localities, ranging from *ca* 790 mm at Derby to *ca* 1160 mm at Anna Plains. This suggests that variations in sex change in *P. macrochir* among localities reflect differences in environmental conditions at those localities.

The difference of 365 mm between the smallest and greatest L_{50}s for sex change in the four populations of *P. macrochir* examined during this study corresponds to as much as *ca* 26% of the total length range of the individuals of this species that were collected. This emphasises very clearly the large variation among the sizes of this threadfin species

at sex change at different locations along the north-western Australian coast. Calculations from data in the literature found that the next largest corresponding percentage difference for size at sex change in a sequentially hermaphroditic species was the 18% recorded by Licandeo *et al*. (2006) for populations of the protandrous notothenioid *Eleginops maclovinus*, in widely-spaced locations around South America. The differences among the populations of this notothenioid species related to latitude, with sex change occurring at longer lengths at higher latitude. As the L_{50}s were most similar in the case of the two most latitudinally separated locations of *P. macrochir*, *i.e.* Derby and Eighty Mile Beach, sex change was not likewise related to latitude in this threadfin species.

The length at sex change of the protandrous centropomid *Centropomus undecimalis* also varies substantially with region, with the L_{50}s for this variable for populations on the west and east coasts of southern Florida differing by as much as *ca* 160 mm (Taylor *et al*., 2000). This difference was considered to reflect mainly a faster rate of growth on the east coast as fish changed sex at the same age on both coasts (Taylor *et al*., 2000). In contrast, and as pointed out above, both the lengths and age of *P. macrochir* at sex change differ markedly among the four populations investigated.

As with *C. undecimalis*, much of the differences in length at sex change of populations of the Barramundi *L. calcarifer* could be attributed to variations in growth rates (Davis, 1982), the individuals in some populations of this protandrous latid become precociously mature and change sex at a younger age and shorter length (Davis, 1984, 1986). As there appears to be only a low level of gene flow among sub-populations of *L. calcarifer,* Davis (1984) attributed the presence of populations with the latter characteristics to differences between the genetic composition of those and other more typical populations. As allozyme and mitochondrial DNA studies have demonstrated that, like Barramundi, populations of *P. macrochir* across much of northern Australia are genetically discreet (Keenan, 1997; Chenoweth & Hughes, 2003), it is possible that the marked differences in the lengths and ages at sex change of individuals in the various populations of *P. macrochir* partly reflect genetic differences.

Evidence that there may be some genetic isolation between north-western Australian populations of *P. macrochir* is provided by the presence of morphological differences between individuals from Derby on the Kimberley coast and those at Roebuck Bay, Anna

Plains and Eighty Mile Beach on the Canning coast. For example, hyperostosis, particularly of the first dorsal-fin pterygiophore (**Plate 5.10**), which is an heritable character indicative of genetic isolation (Smith-Vaniz *et al*., 1995), was found in the vast majority of individuals from Derby, whereas it was never observed at the other three localities.

5.4.4. Spawning period and mode

The presence of females of *E. tetradactylum* with mature ovaries (stage V/VI) in each month between August and January implies that this species spawns between late winter and mid summer. This conclusion is consistent with the fact that the mean monthly GSIs of females were greatest between September and December. The above spawning period of *E. tetradactylum* in north-western Australia is similar to that recorded for this species on the east coast of Queensland, where spawning peaks in October to December (Stanger, 1974; Russell, 1988). In contrast, the spawning of *E. tetradactylum* in the Gulf of Carpentaria in northern Australia peaks slightly earlier, *i.e.* during late winter and early spring (McPherson, 1997).

The protracted spawning season for *E. tetradactylum* in north-western Australia parallels the situation for this species in Indian waters, where fish with mature ovaries are also present for six months or more (Karandikar & Palekar, 1950; Sarojini & Malhotra, 1952; Patnaik, 1970). However, spawning in Indian populations of *E. tetradactylum* has two peaks which are separated by a period of approximately four months and consequently result in well separated "early" and "late" peaks of recruitment (Karandikar & Palekar, 1950; Patnaik, 1970). The trends exhibited by the monthly values for the GSIs of female *E. tetradactylum* suggest that, in north-western Australia, the spawning of this species peaks in September and November, a view consistent with the length-frequency distributions of 0+ age class (Chapter 6).

Although a combination of poor weather in November and the cessation of commercial fishing in November and December meant that it was only possible to obtain one large female of *P. macrochir*, mean monthly GSIs for females still strongly indicated that spawning occurred between September and January. This conclusion is broadly

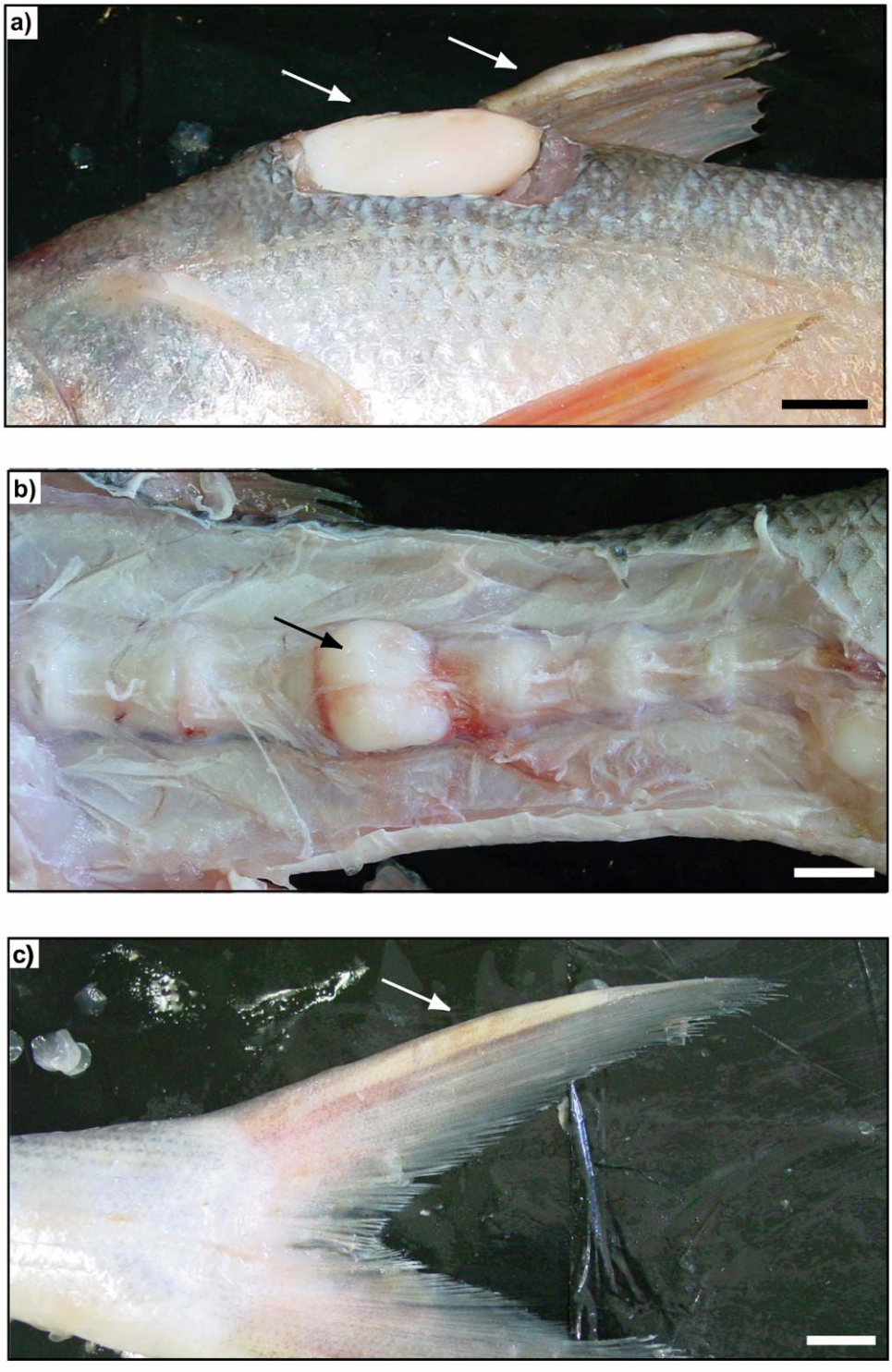

Plate 5.10. Individuals of *Polydactylus macrochir* collected in King Sound near Derby exhibiting examples of hyperostosis (arrows) of the a) first dorsal-fin pterygiophore and spines, b) vertebrae and c) caudal-fin rays. Scale bars in (a), (b) and (c) = 20, 10 and 20 mm, respectively.

consistent with the presence of elevated mean monthly GSIs for males caught between and October and December. An early spring to mid summer spawning period is slightly later than that of this species in the Gulf of Carpentaria, where spawning is estimated as peaking in late winter to early spring (McPherson, 1997). Although Russell (1988) caught very few mature females of *P. macrochir* in his study, he concluded from data for males that this threadfin species spawns in October to March in eastern Queensland.

The lack of a marked discontinuity in the frequency distributions for the diameters of each of the sequential stages in the development of oocytes in stage VI ovaries of both *E. tetradactylum* and *P. macrochir* provided overwhelming evidence that these two threadfin species have indeterminate fecundity, *i.e.* there is continuous development and maturation of oocytes throughout the spawning period. Although this conclusion differs from those reached by Stanger (1974) and Karandikar & Palekar (1950) for *E. tetradactylum* in Queensland and India, respectively, it does agree with those of other workers for other threadfin species (Karekar & Bal, 1960). The presence of both post-ovulatory follicles and yolk granule oocytes with migrating nuclei in individual mature ovaries of both threadfin species strongly suggests that these species spawn on several occasions and within relatively short time intervals, which is consistent with the repetitive spawning that has been observed in *E. tetradactylum* and other threadfin species under aquaculture conditions (May *et al*., 1979; Chao *et al*., 1994).

There was evidence that the spawning of *E. tetradactylum* and *P. macrochir* was related to lunar periodicity. For example, counts of daily rings on the otoliths of juveniles suggest that the juveniles of those two species were spawned very close to the new moon (Chapter 6) and all females of *P. macrochir* with spawning ovaries (stage VI) were caught around the time of the new moon. Other polynemids have been shown to have lunar-related patterns of abundance, with for example, *Polydactylus plebius* being most abundant in the nearshore waters of Madagascar during the period of the new moon (Laroche *et al*., 1997). Lunar periodicity in spawning, which has been documented as occurring in the polynemid *Polydactylus sexfilis* (May *et al*., 1979) and is common amongst teleosts (*e.g.* Greeley *et al*., 1986; Hoque *et al*., 1999; Hesp & Potter, 2003), is a strategy presumably employed to maximise the tidal dispersal of eggs and larvae (Johannes, 1978).

The trends in the GSIs of sequential size classes of mature male *P. macrochir* revealed that small males, *i.e.* those <500 mm in length, made a disproportionately higher expenditure of reproductive effort than larger males, *i.e.* those >700 mm. Large testes size is indicative of a high degree of sperm competition and is often a characteristic of group spawning fish (Parker *et al*., 1996; Stockley *et al*., 1997; Stoltz *et al*., 2005). The uneven reproductive expenditure by male *P. macrochir* suggest unequal levels of sperm competition (Parker, 1990a, b) and may reflect a shift from spawning as part of large groups towards small group or pair spawning as the males attain lengths approaching those of females. Such a strategy parallels that observed in some harem forming protogynous species where non-dominant "sneaker" males, which possess relatively large testes, attempt to compete for spawning opportunities against larger dominant males (Gross, 1996; Taborsky, 1998; Oliveira *et al*., 2005). The social impetus for the adoption of a broadcast spawning strategy by small male *P. macrochir* could reflect predation avoidance, as small threadfin (up to 355 mm TL) were found in the stomachs of large *P. macrochir* and thus small males are subject to cannibalism by females and large males during the spawning period.

5.4.5. Habitats used by threadfin for spawning

Analysis of the numerous samples collected using seine and gill nets and by commercial and recreational fishers enabled the types of habitat occupied by *E. tetradactylum* and *P. macrochir* during their life cycles to be elucidated. Thus, these data, together with the absence of these species in catches obtained in offshore waters (Newman *et al*., 2003), demonstrate that *E. tetradactylum* and *P. macrochir* live predominantly over unvegetated substrates in nearshore, shallow waters. However, *P. macrochir* tends to live, to a greater extent, than *E. tetradactylum*, in areas where the substrate contains larger amounts of organic material and fine particles. The presence of individuals with mature gonads in nearshore waters indicates that these waters act as a spawning as well as nursery area for *E. tetradactylum* and *P. macrochir* in north-western Australia. The spawning of *E. tetradactylum* in nearshore waters in north-western Australia parallels the situation with this species in Indian waters, where the majority of spawning occurs in coastal marine,

rather than estuarine environments (Sarojini & Malhotra, 1952; Jones & Sujansingani, 1954; Muthiah, 1985).

Although *P. macrochir* also spawns in nearshore waters, females with spawning gonads (stage IV) were caught only at Roebuck Bay and Anna Plains and thus this species appears to be more particular than *E. tetradactylum* in selecting its spawning locations. Further evidence that these two locations constitute important spawning locations was provided by the collection of substantial numbers of newly-recruited juvenile *P. macrochir* in seine net catches at Anna Plains and by the greater contribution of such recruits to the diets of adult *P. macrochir* at Roebuck Bay and Anna Plains than at more sandy sites including Port Smith, Eighty Mile Beach or Cape Keraudren (unpub. data).

The fact that newly-recruited juveniles of *P. macrochir* were found almost exclusively in fine sediment habitats, *i.e.* at Roebuck Bay and Anna Plains, demonstrates that this type of habitat constitutes an important nursery area for this species. Blaber (1980) also noted that juvenile polynemids occurred only over muddy substrates in open bay habitats in the Trinity Inlet estuarine system in northern Queensland. Mudflat habitats play an important nursery function for other juvenile fish (Morrison *et al*., 2002). The nursery importance of the intertidal habitats at Roebuck Bay and Anna Plains presumably reflects, in part, the presence of substantial amounts of food, which is consistent with the fact that both of these locations are known to have an extremely abundant and diverse intertidal invertebrate fauna (Piersma *et al*., 1999, 2002).

6. Size and age compositions, growth rates, mortality and stock assessment of *Eleutheronema tetradactylum* and *Polydactylus macrochir*

6.1. Introduction

The ultimate aim of fisheries managers is to ensure the long-term sustainability of fish resources. For this to be successful, it is essential that management policies are developed using reliable biological data for the targeted species. The types of data required include sound quantitative information on size and age compositions, growth and mortality (Beverton & Holt, 1957; Appledoorn, 1996; Campana & Thorrold, 2001; Hall *et al*., 2004). The above types of data can then be incorporated into the age-structured models that are frequently employed for stock assessments (*i.e.* Megrey, 1989; Xiao, 2000; Aubone; 2004). Such models enable managers to assess and predict the impact of different levels of exploitation for harvested fish populations for setting sustainable fishing levels (eg. Murray & Gaughan, 2003; Andrews *et al*., 2004; Hjermann *et al*., 2004). For many species, the empirical data required to undertake a stock assessment are limited and, in these cases, per-recruit analyses are commonly employed to estimate potential yields at various levels of exploitation (Bannerot *et al.*, 1987; Buxton, 1992; Punt *et al.*, 1993).

Accurate estimates of the age composition, growth parameters and mortality of a stock are dependent on reliable estimates of the ages of representative individuals of that stock (Quinn & Deriso, 1999; Campana & Thorrold, 2001; Francis & Campana, 2004). As age determination techniques are normally based on counts of growth zones in hard structures such as otoliths (Ricker, 1979; Beamish & McFarlane, 1987; Casselman, 1990), it is crucial to validate that these growth zones are formed annually and this should thus constitute an essential part of any ageing study (Beamish & McFarlane, 1983; Casselman, 1987; Campana, 2001). Furthermore, determination of the timing of annulus formation, and particularly of the first growth zone laid down during early life, is essential in establishing a reliable age for individual fish (Campana, 2001). Failure to perform rigorous validation can result in ageing errors, leading to inaccurate estimates of growth parameters and mortality and may thus ultimately result in poor management decisions

and unsustainable exploitation of a fish stock (Beamish & McFarlane, 1983; Smith *et al*., 1995).

Although threadfin species are highly regarded for their eating qualities and form the basis of important commercial, recreational and subsistence fisheries, few attempts have been made to carry out stock assessments on these species. However, the yields of some threadfin species in certain regions have declined so markedly in recent years that the commercial fisheries for those stocks have virtually collapsed (Abohweyere, 1989; Szyper *et al*., 1991; Bensam & Menon, 1994; Cheung & Sadovy, 2004; Kizhakudan & Kizhakudan 2005). The susceptibility of certain threadfin species to fishing pressure has been attributed mainly to the consequence of their being protandrous hermaphrodites, *i.e*. maturing first as males and then changing sex to females with increasing size and age (Bensam & Menon, 1994; Friedlander & Ziemann, 2003; Poepoe *et al*., 2003). It is more difficult to develop reliable per-recruit models for hermaphroditic species than gonochoristic species as it requires, in addition to accurate age determination, a thorough understanding of the relationship between sex change and the size and age of the fish involved (*e.g.* Buxton, 1992; Punt *et al.*, 1993; Hesp *et al*., 2004; Heppell *et al*., 2006).

The Blue Threadfin *Eleutheronema tetradactylum* grows relatively rapidly in Australian waters, reaching lengths of *ca* 420 mm within two years (Stanger, 1974), and attains a maximum length and age of *ca* 1050 mm and 7 years in the Gulf of Carpentaria (Bibby & McPherson, 1997). In Indian waters, *E. tetradactylum* is known to attain much greater lengths, *i.e.* >1500mm in the Mangalore region of India (Motomura *et al*., 2002a) and reported to reach 1800-2000mm in other parts of India (Gopalakrishnan, 1972; Krishnamurthy & Jeyaseelan, 1981; Feltes, 1999). However, the age of those large Indian specimens is unknown. The King Threadfin *Polydactylus macrochir* also exhibits rapid early growth in Australian waters reaching total lengths in excess of 400 mm within two years (Garrett, 1992; Bibby & McPherson, 1997). Unconfirmed reports suggest that *P. macrochir* may live for greater than 20 years and attain fork lengths and total weights of *ca* 1700 mm and 40kg, respectively (Kailola *et al*., 1993).

McPherson (1997), in the only yield per recruit (YPR) analysis for *Eleutheronema tetradactylum*, concluded that the stocks of this species in the Gulf of Carpentaria (Queensland) were unlikely to be over-exploited. However, the rate of mortality

attributable to fishing (*F*) for *E. tetradactylum* was not estimated and thus the status of that stock remains unknown. Furthermore, McPherson (1997) was unsuccessful in deriving an estimate of *F* for *Polydactylus macrochir* as the amount of biological data were insufficient to conduct YPR analysis for that species.

More recently, Welch *et al*. (2002) attempted to fit various biomass dynamic models to historical catch data for Gulf of Carpentaria and Eastern Queensland stocks of *E. tetradactylum* and *P. macrochir,* but these models gave a relatively poor fit to the data and resulted in unrealistic estimates of maximum sustainable yield. Welch *et al*. (2002) was able to determine an estimate of the maximum constant yield (MCY) for each stock of *E. tetradactylum* and *P. macrochir* and suggested that the fisheries for each of these species in both the Gulf of Carpentaria and Eastern Queensland were over-exploited. However, the MCY analysis performed in that study incorporated estimates of natural mortality (*M*) for each species, that were inferred to be analogous with the estimates of total mortality (*Z*) derived by refitting the equation of Hoenig (1983). Although such an assumption may be valid for the lightly-fished stocks of some long-lived fishes (Gunderson *et al*., 2003; Hewitt & Hoenig, 2005), it is inappropriate for these two threadfin species as i) they are apparently relatively short lived (Stanger, 1974; Russell, 1988; Garrett, 1992; Bibby & McPherson, 1997) and ii) it is unlikely their stocks are lightly-fished (Welch *et al*., 2002; Newman & Harvey, 2005).

Despite the importance of *E. tetradactylum* and *P. macrochir* to commercial, recreational and indigenous fishers in north-western Australia (see Chapter 1.3), there has been no attempt to collect the types of data, such as size and age composition, growth parameters and estimates of mortality, required to undertake per recruit analysis of stocks of either threadfin species in Western Australia. Thus, the individual aims of this study, which were the same for both *E. tetradactylum* and *P. macrochir*, were as follows. 1. Establish a reliable estimate of the length-weight relationship for use in stock assessment models. 2. Validate that opaque zones are laid down in otoliths annually and that these growth zones can thus be used to reliably age fish. 3. Determine the size and age compositions and growth characteristics. 4. Estimate total, natural and fishing mortality. 5. Estimate the current level of yield per recruit, spawning biomass per recruit and spawning potential ratio.

6.2. Methods

6.2.1. Age and growth

The methods and sampling regime employed to collect threadfin are outlined in Chapter 5.2.1. The sagittal otoliths were removed from each fish, cleaned, dried and stored in paper envelopes. Whole otoliths from a subsample of 100 individuals of each species, which covered the range of lengths of those species, were immersed in methyl salicylate and examined microscopically under reflected light against a black background and the number of their opaque zones recorded. The same otoliths were mounted in clear epoxy resin and cut transversely into *ca* 500 µm thick sections through their primordia using an Isomet Buehler low speed diamond saw. The sections were cleaned and mounted on slides using DePX mounting medium and examined microscopically under reflected light.

The opaque zones on each otolith, both prior to and after sectioning of that otolith, were counted without knowledge of the size or capture date of the fish from which that otolith had been removed. Although the number of opaque zones visible in each otolith of each species over the entire size range of fish caught was the same after sectioning as before sectioning, the opaque zones of otoliths with larger numbers of opaque zones were more readily observed in sectioned otoliths (**Plate 6.1**). Thus, opaque zones were counted using whole otoliths when that otolith contained six or less zones, but employed sectioned otoliths when that otolith contained more than six zones. The number of opaque zones on otoliths was recounted by a second otolith reader. There was no discrepancy between readers in the counts made of opaque zones on individual otoliths.

Validation that opaque zones on the otoliths of both species are formed annually was undertaken using marginal increment analysis. For this purpose, measurements were made of the marginal increment, *i.e.* the distance from the outer edge of the single or outermost opaque zone to the edge of the otolith. The marginal increment (L_1) was then expressed as a proportion of a) the distance between the primordium and the outer edge of the opaque zone (L_2 in **Plate 6.2**), when only one such zone was present, or b) the distance between the outer edges of the penultimate and outermost opaque zones (L_2 in **Plate 6.3**), when more than one such zone was present. All measurements, which were made perpendicular to the opaque zones and along the long posterior axis of the otolith, were recorded to the nearest 0.01 mm using the Leica computer image managing package

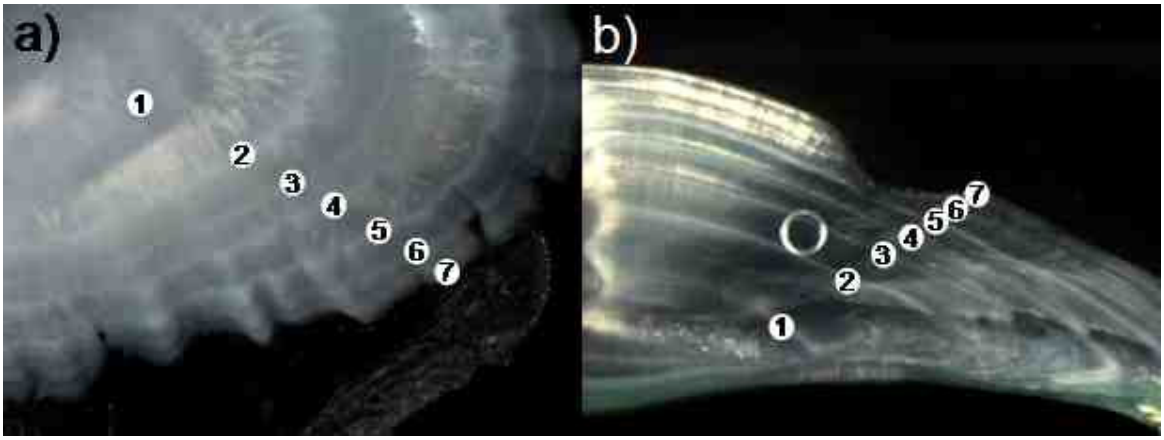

Plate 6.1. Otolith of a *Polydactylus macrochir* of 1143 mm TL photographed a) whole and b) after sectioning. Seven opaque zones are visible on the otolith, both prior to and after sectioning. Photographs were taken microscopically and using reflected light.

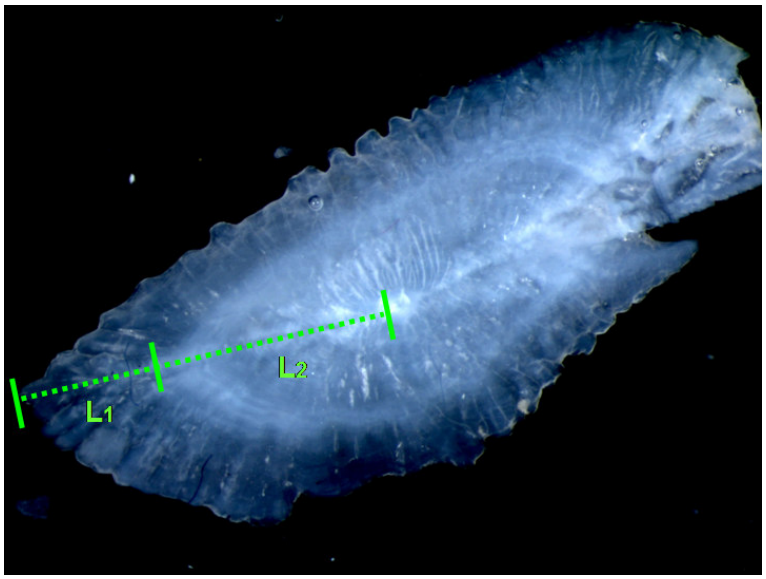

Plate 6.2. A whole otolith of *Eleutheronema tetradactylum* (383 mm TL) showing the measurements used for marginal increment analysis when only one opaque zone (annulus) is present. L_1 = the marginal increment, *i.e.* distance between the outer edge of the opaque zone and the edge of the otolith; L_2 = distance between the primordium and the outer edge of the opaque zone.

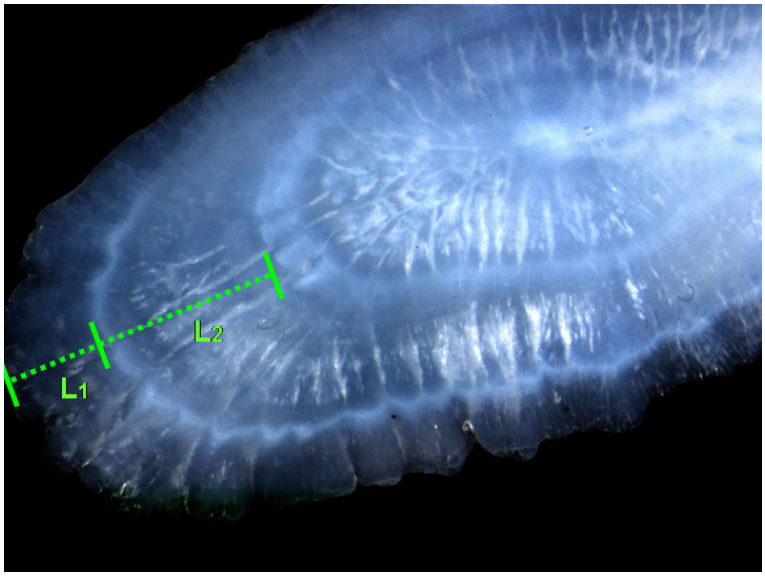

Plate 6.3. Part of a whole otolith of *Polydactylus macrochir* (827 mm TL) showing the measurements used for marginal increment analysis when more than one opaque zone (annulus) is present. L_1 = the marginal increment, *i.e.* distance between the outer edge of the outermost opaque zone and the edge of the otolith; L_2 = distance between the outer edges of the penultimate and outermost opaque zones.

IM1000 (images were captured using the video and microscope combination outlined in Chapter 5.2.4). A sub-sample of otoliths (*ca* 10-20) from each age class and capture month were subjected to marginal increment analysis. However, the marginal increments were measured without knowledge of the date of capture of the fish from which that otolith had been removed.

Each species was assigned a birth date, which represented the estimated time of peak spawning, determined from the monthly trends exhibited by gonadosomatic indices, gonadal maturity stages and pattern of oocyte development (Chapter 5). Monthly samples of small fish which, from length-frequency distributions, were clearly 0+ fish, were used to confirm that the first opaque zone was laid down in the first winter of life. The length-at-age of each individual of each species at the time of capture was then determined from the number of opaque zones (annuli) on the otoliths and the birth date of that species.

As *E. tetradactylum* and *P. macrochir* both change from male to female with increasing age (Chapter 5), a single von Bertalanffy growth curve was fitted to the lengths at age of the individuals of *E. tetradactylum* and *P. macrochir*. The von Bertalanffy growth equation is $\hat{L}_t = L_\infty\left(1 - e^{-k(t-t_0)}\right)$, where $\hat{L}_t$ is the predicted total length (mm) at age

t years, L_∞ is the mean of the asymptotic length (mm) predicted by the equation, *k* is the growth coefficient (year^{-1}) and t_0 is the hypothetical age (years) at which fish would have a predicted length equal to zero mm. The von Bertalanffy growth curves were fitted by minimizing the sum of squares, using SOLVER in Microsoft Excel™. The data were randomly resampled and analysed to create 1000 sets of bootstrap estimates for the parameters of the von Bertalanffy growth equation. The point estimate for each parameter was taken as the median of the 1000 bootstrap estimates. The 95% confidence limits for the von Bertalanffy growth parameters were calculated as the 2.5 and 97.5 percentiles of the corresponding estimated values.

6.2.2. Mortality

The instantaneous coefficients for total mortality, *Z*, and natural mortality, *M*, for *E. tetradactylum* and *P. macrochir* were estimated employing the approach of Hall *et al.* (2004), which combines the various estimates of *Z* obtained using a combination of i) a regression equation refitted to Hoenig's (1983) fish data, ii) relative abundance (catch curve) analysis and iii) simulation based on the ages of the oldest fish and which ensures that *M* does not exceed *Z*. The following summarises the methods used for deriving each of the individual estimates of mortality and of the method of Hall *et al.* (2004) for combining the various results.

Initially, an estimate of *Z* was obtained for both species using the relationship between total mortality and maximum age, as described by the equation of Hoenig (1983) for fish. This relationship was refitted to the data given for the 82 fish stocks provided in Hoenig (1982). For both *E. tetradactylum* and *P. macrochir*, the maximum recorded ages of 6 and 10, respectively, were then inserted into the Statistical Package for the Social Sciences (SPSS Inc., Chicago III) to obtain point estimates and associated 95% confidence limits, thereby taking into account the uncertainty of the parameter estimates and the variation of the data around the regression line.

A second estimate of *Z* was determined for each species using relative abundance (catch-curve) analysis (Deriso *et al.*, 1985). The age at full recruitment to the exploited stock of each species was determined by developing an age-frequency histogram for both

E. tetradactylum and *P. macrochir*. The mortality estimates were derived from the age classes that were located on the descending limb of the age-frequency distribution to the fishery, and were thus fully-recruited (Ricker, 1975). The catch curves for each species were analysed assuming that Z and the levels of annual recruitment are constant and that the age composition of fully-recruited fish represents a random sample from a multinomial distribution with uniform selectivity from the age of full recruitment (Hall *et al.*, 2004). The value of Z was estimated by maximising the log-likelihood using the SOLVER routine in Microsoft Excel™. The data for each species were randomly resampled with replacement and the resulting samples were analysed to create 10,000 sets of bootstrap estimates. The point estimate of Z was taken as the median of the 10,000 bootstrap estimates. The 95% confidence limits were calculated as the 2.5 and 97.5 percentiles of the corresponding estimated values.

In the case of *E. tetradactylum*, the age data incorporated in the relative abundance (catch-curve) analysis employed those derived from the fish in the large catches obtained by recreational anglers that were fishing between Dampier and Broome. These catches, from which samples were collected randomly, were considered to represent best the population of *E. tetradactylum* in this region. However, as recreational catches of *P. macrochir* were not substantial, the length data for the fish in those catches were supplemented by those recorded by other workers during their tagging experiments on this species and entered in the database maintained by WESTAG. The ages of fish in the latter database were derived from their lengths, using the inverse of the von Bertalanffy growth equation for this species. The data for the study of *P. macrochir* were collected in the region between Dampier and Port Headland by recreational anglers and are thus considered to provide an estimate of total mortality unbiased by the selectivity of the gill nets used in the commercial fishery for this species.

A third estimate of Z was determined for both species using a variation of the simulation approach described by Hall *et al*. (2004), which employed, within each of the samples, the number of fish that were as old or older than a specified age. Thus, for *E. tetradactylum* and *P. macrochir*, the specified ages were 4 and 7, respectively, and the number of fish above those ages were 9 and 7, respectively. The three estimates of Z

derived for each species were then combined, using the Bayesian approach of Hall *et al.* (2004).

Estimates of natural mortality, *M*, for both *E. tetradactylum* and *P. macrochir* were calculated from the relationship between natural mortality, growth and water temperature as described by Pauly (1980). Thus, for each species, the values for k (year^{-1}) and L_∞ (cm TL), derived from the von Bertalanffy growth relationship, and the mean annual surface water temperature (^oC), T, were refitted to Pauly's data for 175 fish stocks using SPSS to obtain point estimates and associated 95% confidence limits for *M*. The mean annual surface water temperature used for both species was 26.9 ^oC, which is the mean temperature derived from data recorded by the Australian Oceanographic Data Centre http://www.AODC.gov.au for the region between Karratha and Broome.

For both *E. tetradactylum* and *P. macrochir,* the Bayesian approach of Hall *et al.* (2004) was used to determine the likelihood for *M*, calculated using the combined likelihood for *Z*, where, for each value of Z, it is assumed there is a uniform probability that $M < Z$. The resulting likelihood for *M* was then combined with the estimate for *M* derived from the Pauly (1980) equation.

A Monte Carlo resampling approach was used to derive estimates of fishing mortality, *F*, for both species. Estimates of *Z* and *M* were randomly resampled, with replacement, from their respective probability distributions (*i.e.* combined *Z* estimate and Pauly (1980) estimate for *M*), but were rejected when corresponding values for *M* were greater than for *Z*. These values were used to produce 5000 estimates for *F*, determined using the equation $F = Z - M$. The point estimate of *F* and the associated 95% confidence limits were taken as the median value and the 2.5 and 97.5 percentiles of the 5000 estimates derived from the re-sampling analysis.

6.2.3. Yield and spawning biomass per recruit

The yield per recruit (YPR) and spawning stock biomass per recruit (SSB/R) for both species were calculated assuming knife-edge recruitment at the age of full recruitment t_c (years), constant total mortality for fully-recruited fish and a maximum age of 50 years. Yield per recruit for each species was calculated as,

$$YPR = \sum_{a=t_c}^{50} \frac{F}{Z}(1 - e^{-Z})W_a \exp(-Za)$$

where F refers to the estimated current level of fishing mortality and where W_a, the total body weight (kg) at age a (years), was determined from the predicted length at age determined using the von Bertalanffy growth curve for each species and employing the relationship between total body weight (g) and length (mm) for each species. The values for the fishing mortality that maximises YPR, $F_{\max,}$ and that at which the derivative of YPR with respect to F is one tenth of that at the origin, $F_{0.1,}$ were estimated numerically in Excel™. These two values were used as the biological reference points for fishing mortality for each species against which the estimate of the current level of fishing mortality was compared (Hilborn & Walters, 1992; Haddon, 2001).

The SSB/R for the females and males of each species was calculated as,

$$SSB / R = \sum_{a=t_c}^{50} W_a P_{sex,a} P_{mat,a} \exp(-Za) .$$

W_a, the total body weight at age a, was determined from the length at age predicted using the von Bertalanffy growth curve and employing the total body weight (g) to length (mm TL) relationship. As *E. tetradactylum* and *P. macrochir* are both protandrous hermaphrodites (Chapter 5), $P_{sex,a}$, the proportion of that sex at age a, was determined using the logistic function relating the proportion at each length of that sex and the von Bertalanffy growth equation for both species. Therefore, $P_{sex,a}$ for males was calculated as 1 minus the proportion of fish that had changed sex from male to female.

Estimates for the current levels of YPR and SSB/R were determined for each of the 5000 values generated for F derived from the Monte Carlo resampling procedure. The point estimates and associated 95% confidence limits for the current level of YPR and SSB/R for both species were taken as the median and 0.025 and 0.975 percentiles of the resulting YPR and SSB/R values. The spawning potential ratio, SPR, was calculated as the ratio of SSB/R at a specified level of fishing mortality to that estimated for an unfished population (Goodyear, 1993).

6.3. Results

6.3.1. Length / weight relationships for threadfin species

Samples collected with seine and gill nets and from commercial and recreational fishers provided a wide size range of both *Eleutheronema tetradactylum* and *Polydactylus macrochir* (**Plates 6.4, 6.5**). The relationships between wet weight (*W*) and total length (*TL*) of *Eleutheronema tetradactylum* and *Polydactylus macrochir* were:

E. tetradactylum $W = 1.736\text{x}10^{-6} \text{ x } TL^{3.262}$ ($R^2 = 0.989$, $n = 682$)

P. macrochir $W = 8.848\text{x}10^{-6} \text{ x } TL^{2.963}$ ($R^2 = 0.974$, $n = 872$)

The relationships between total length (*TL*) and caudal fork length (*FL*) of *E. tetradactylum* and *P. macrochir* were:

E. tetradactylum $TL = (0.8381 \text{ x } FL) - 1.6604$ ($R^2 = 0.999$, $n = 895$)

P. macrochir $TL = (0.8413 \text{ x } FL) - 6.4416$ ($R^2 = 0.999$, $n = 1089$)

6.3.2. Validation that opaque zones on otoliths are formed annually

The mean monthly marginal increments on *E. tetradactylum* otoliths with 1, 2 and 3 or more opaque zones rose from low values in January to high values in July to October and then declined precipitously to their minima in November or December (**Figure 6.1**). The trends exhibited by the mean monthly marginal increments on the otoliths of *P. macrochir,* irrespective of the number of opaque zones, were similar to those of *E. tetradactylum,* with values being least in late spring and early summer and greatest during winter and early spring (**Figure 6.2**).

6.3.3. Length-frequency distributions of the different age classes

During spring, the lengths of the 0+ age class of *E. tetradactylum* collected from nearshore waters at Anna Plains and Eighty Mile Beach, where the 21.5 m seine net was used, ranged widely, *i.e.* from 20 to 137 mm, and was bimodal (**Figure 6.3a**). The lengths of the 0+ cohort in summer, autumn and winter were likewise wide, but still did not overlap those of the 1+ or other age classes in any of these seasons. The maximum total lengths of 0+ fish during these seasons were 194, 276 and 299 mm, respectively. The lengths of the 1+ age class ranged from 167–310 mm in spring and those of the larger 1+ fish overlapped

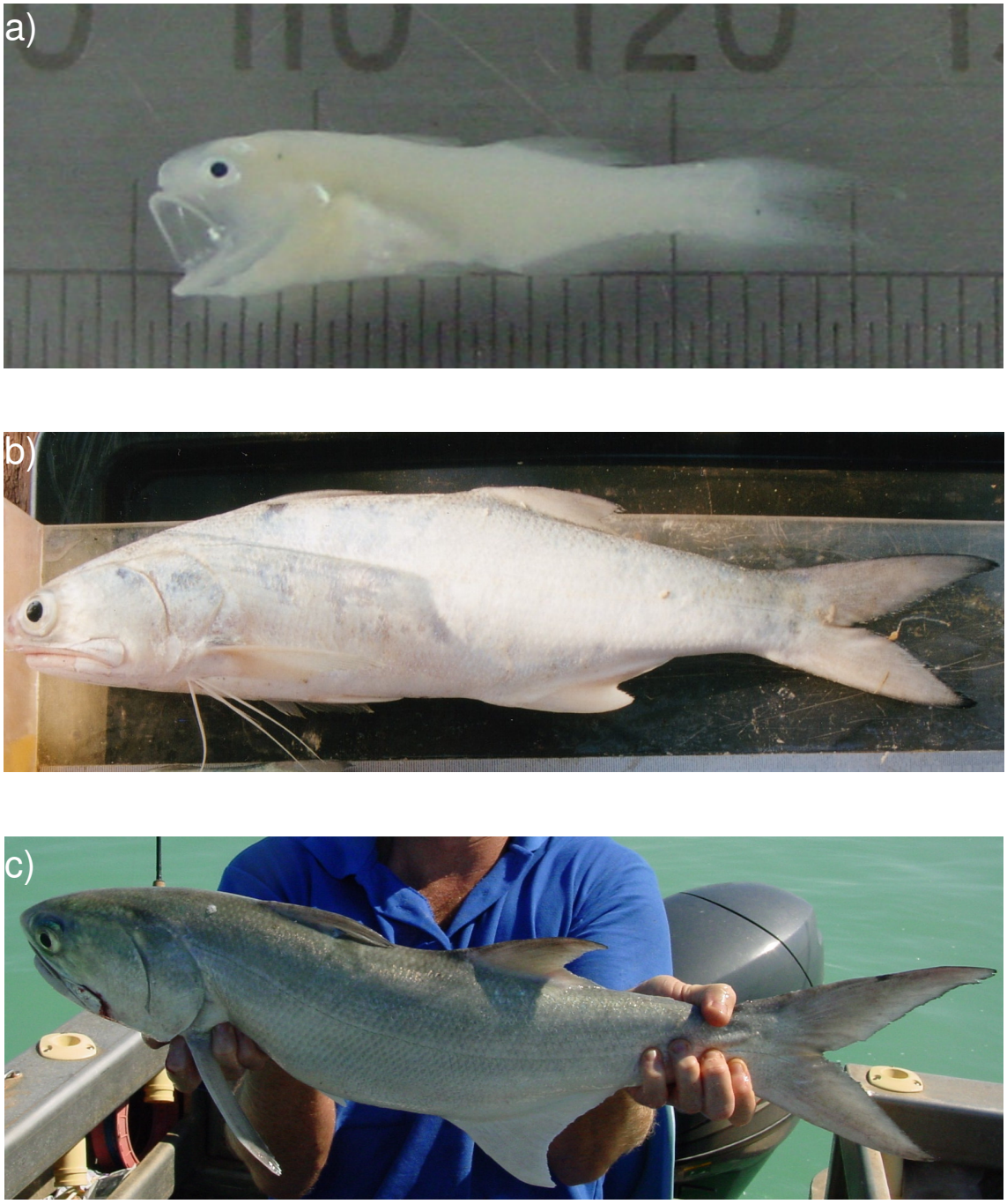

Plate 6.4. Individuals of *Eleutheronema tetradactylum* caught by a) seine netting at Anna Plains (21 mm TL), b) gill netting at Eighty Mile Beach (420 mm TL) and c) angling at Roebuck Bay (712 mm TL).

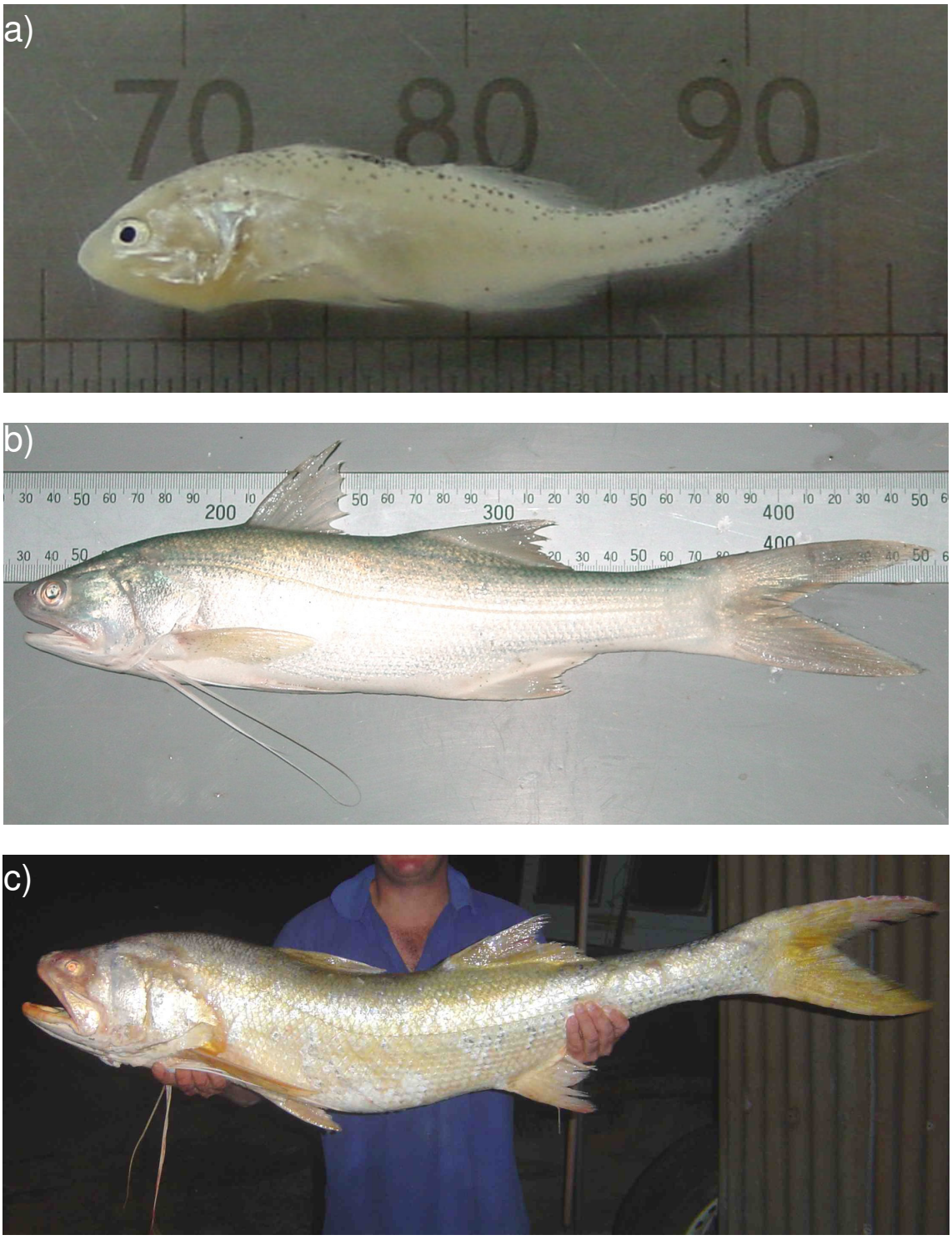

Plate 6.5. Individuals of *Polydactylus macrochir* caught by a) seine netting at Anna Plains (30 mm TL), b) seine netting at Eighty Mile Beach (331 mm TL) and c) commercial gill net catches at Anna Plains (1393 mm TL).

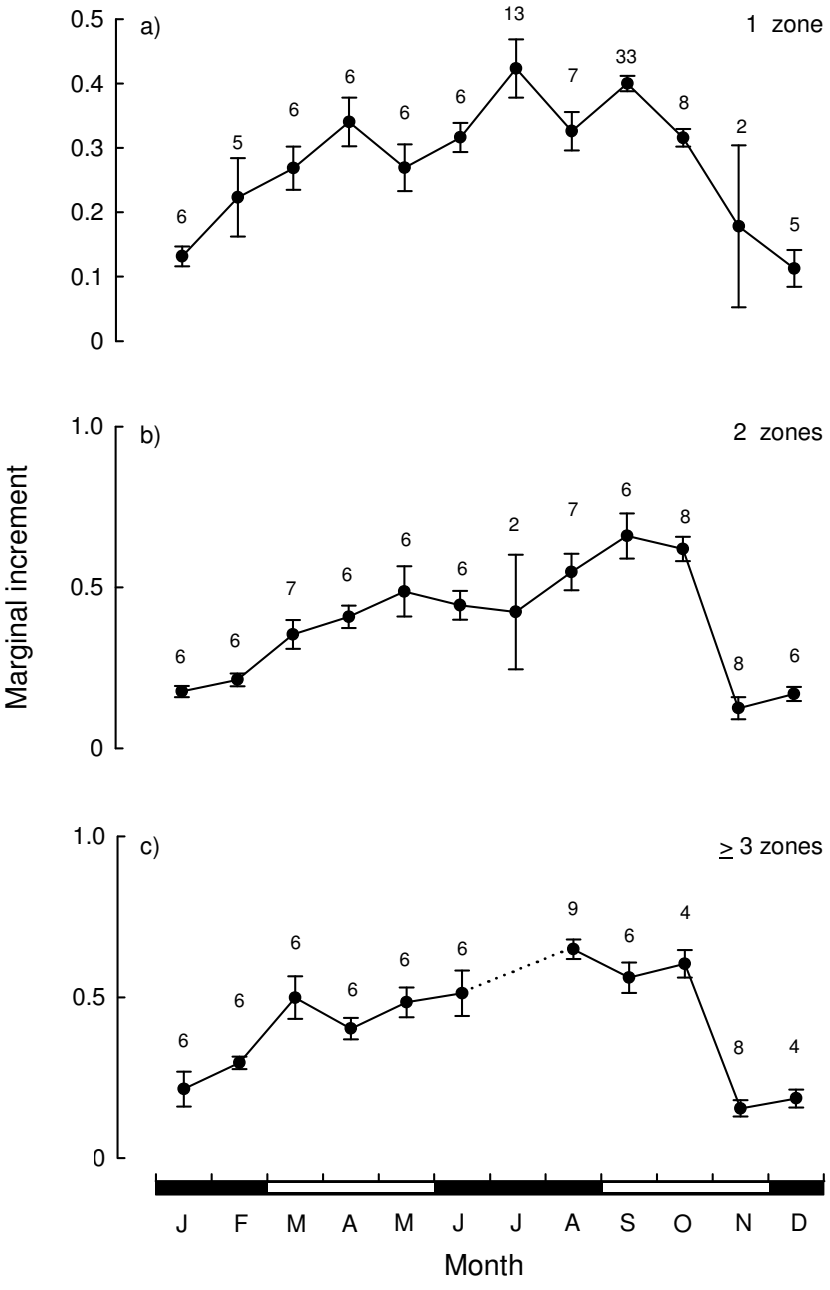

Figure 6.1. Mean monthly marginal increments (±1SE) for the otoliths of *Eleutheronema tetradactylum* with different numbers of opaque zones.

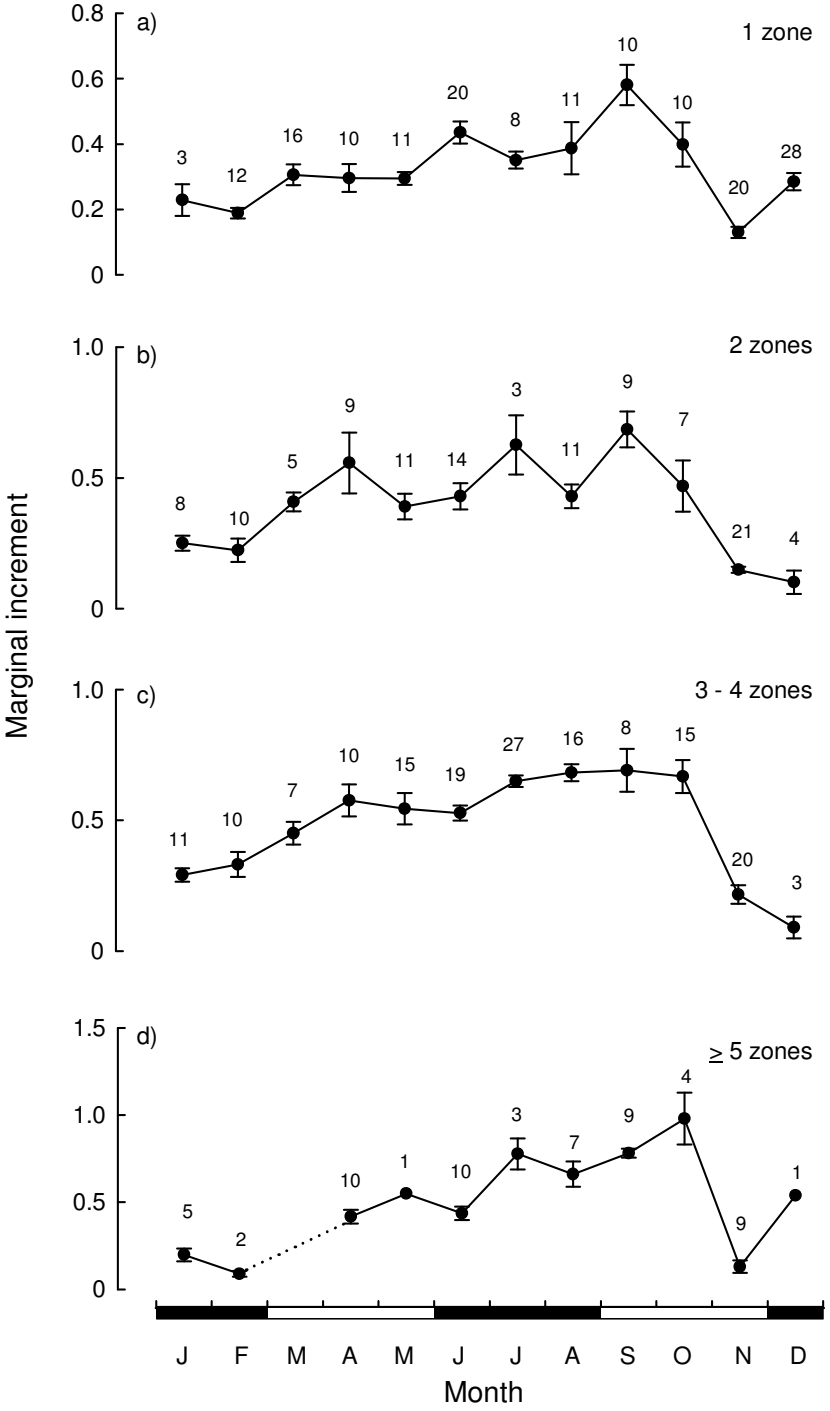

Figure 6.2. Mean monthly marginal increments (±1SE) for the otoliths of *Polydactylus macrochir* with different numbers of opaque zones.

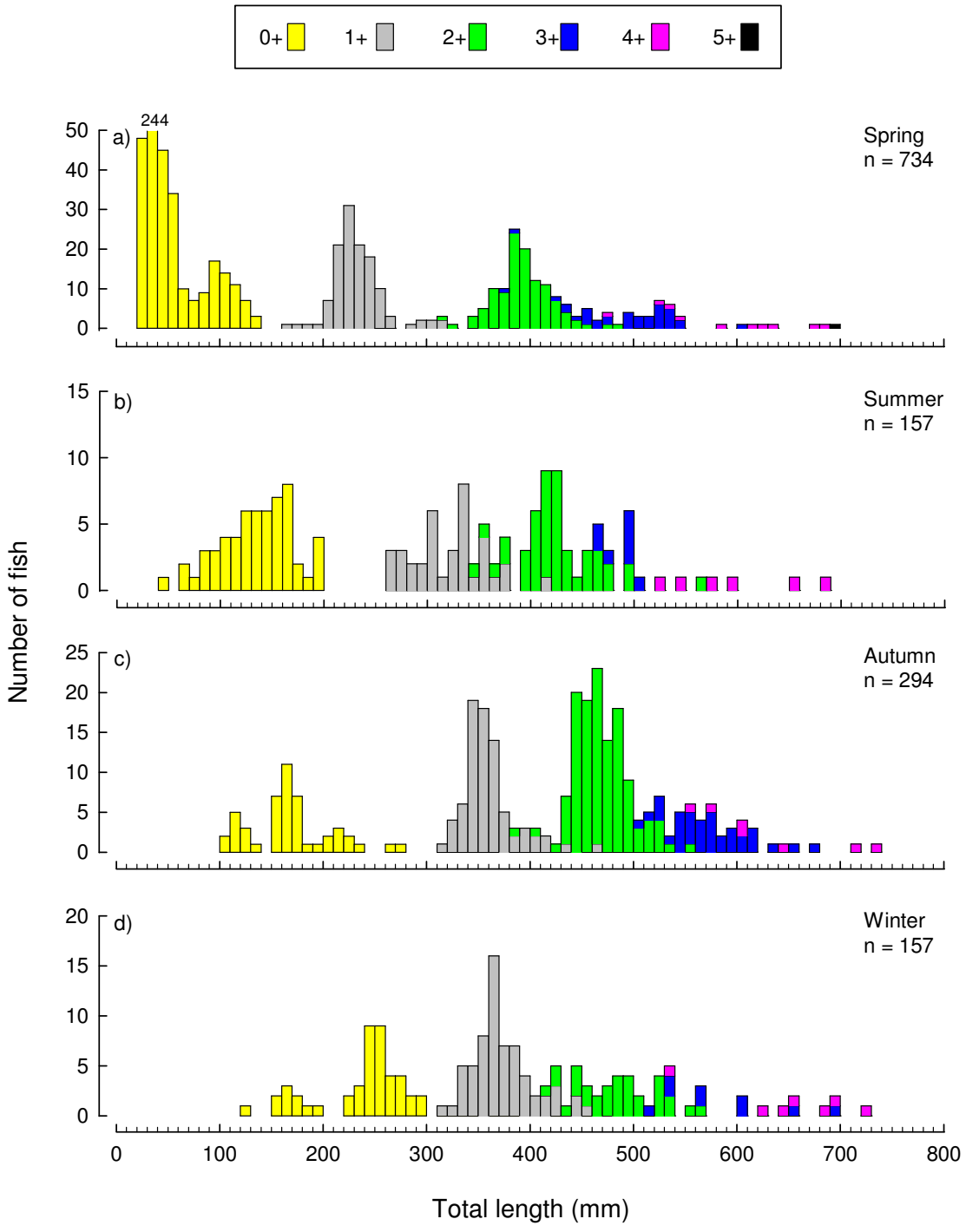

Figure 6.3. Length-frequency distributions of the different age classes of *Eleutheronema tetradactylum* in catches obtained with seine and gill nets and by recreational fishers in nearshore waters at Anna Plains and Eighty Mile Beach during a) spring, b) summer, c) autumn and d) winter.

those of the smaller 2+ fish in each season (**Figure 6.3**). By winter, the lengths of the 1+ age class ranged from 312 mm to 452 mm (**Figure 6.3d**). The lengths of the 2+ cohort increased from 317–488 during spring to 415-562 mm by winter. Furthermore, in each season, the lengths of the larger 2+ fish overlapped those of the smaller 3+ fish. (**Figure 6.3**)The length range of 0+ *E. tetradactylum* collected in nearshore waters of north-western Australia was wide, ranging from 20 to 311 mm (**Figure 6.4**). The modal length classes for the 1+, 2+, 3+ and 4+ cohorts increased progressively from 350-374 to 450-474, 525-549 and 600-624 mm, respectively. The total length of the eight five year old individuals of *E. tetradactylum* ranged from 675 to 793 mm (**Figure 6.4**).

The new 0+ recruits of *P. macrochir* were first collected from nearshore waters in spring, with the lengths of most of these lying between 20 and 80 mm (**Figure 6.5a**). Although only a few 0+ fish were caught in summer, this age class was well represented in autumn and winter, when their lengths ranged from 185 to 397 mm (**Figure 6.5d**). The lengths of the 1+ cohort ranged widely from 193 to 437 mm in spring and, by winter had reached 280 to 599 mm. The 2+ cohort could also be followed throughout the year, with lengths ranging from 363 to 680 mm in spring and 465 to 920 mm by winter. Although few 3+ fish were less than 500 mm and few 4+ fish were less than 700 mm, there was considerable overlap between the upper and lower lengths of the individuals in all age classes between 3+ and 6+ (see **Figure 6.5**).

The total lengths of 0+ *P. macrochir* ranged from 19 to 441 mm and produced a modal length class at 250-299 mm (**Figure 6.6**). The lengths of successive age classes increased progressively and particularly between the 0+ and 4+ age classes. The remaining cohorts continued to increase in length with all six of the 8+ and 9+ fish collectively exceeding 1250 mm in length (**Figure 6.6**). The largest individual collected during the study, which belonged to the 9+ cohort, had a total length of 1393 mm.

6.3.4. von Bertalanffy growth curves

The von Bertalanffy growth curve provided a very good fit to the lengths at age of the individuals of *E. tetradactylum* from the four regions sampled (**Figure 6.7**), a feature reflected in the high value of 0.967 for the coefficient of determination (**Table 6.1**). The

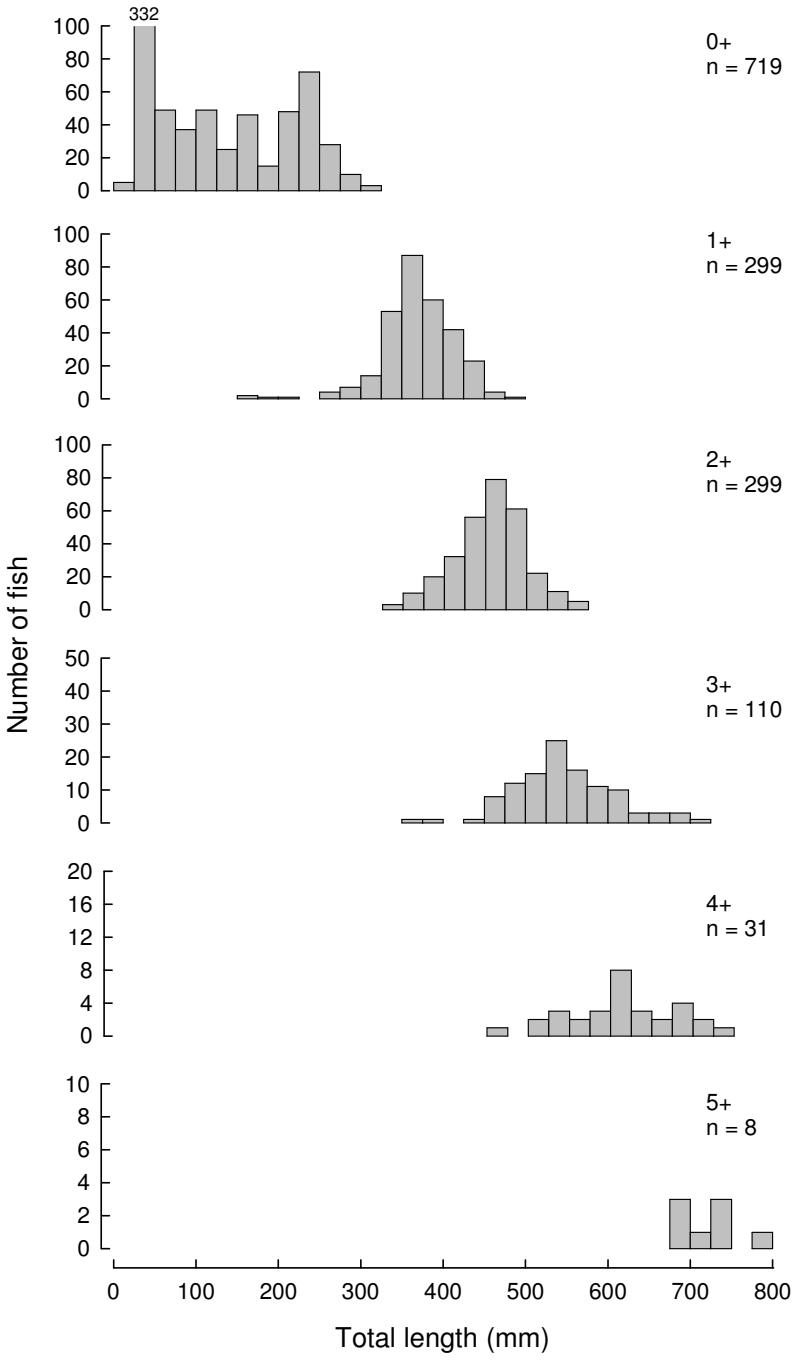

Figure 6.4. Length-frequency distributions of the different age classes of *Eleutheronema tetradactylum* caught with seine and gill nets and by recreational and commercial fishers in nearshore waters of north-western Australia.

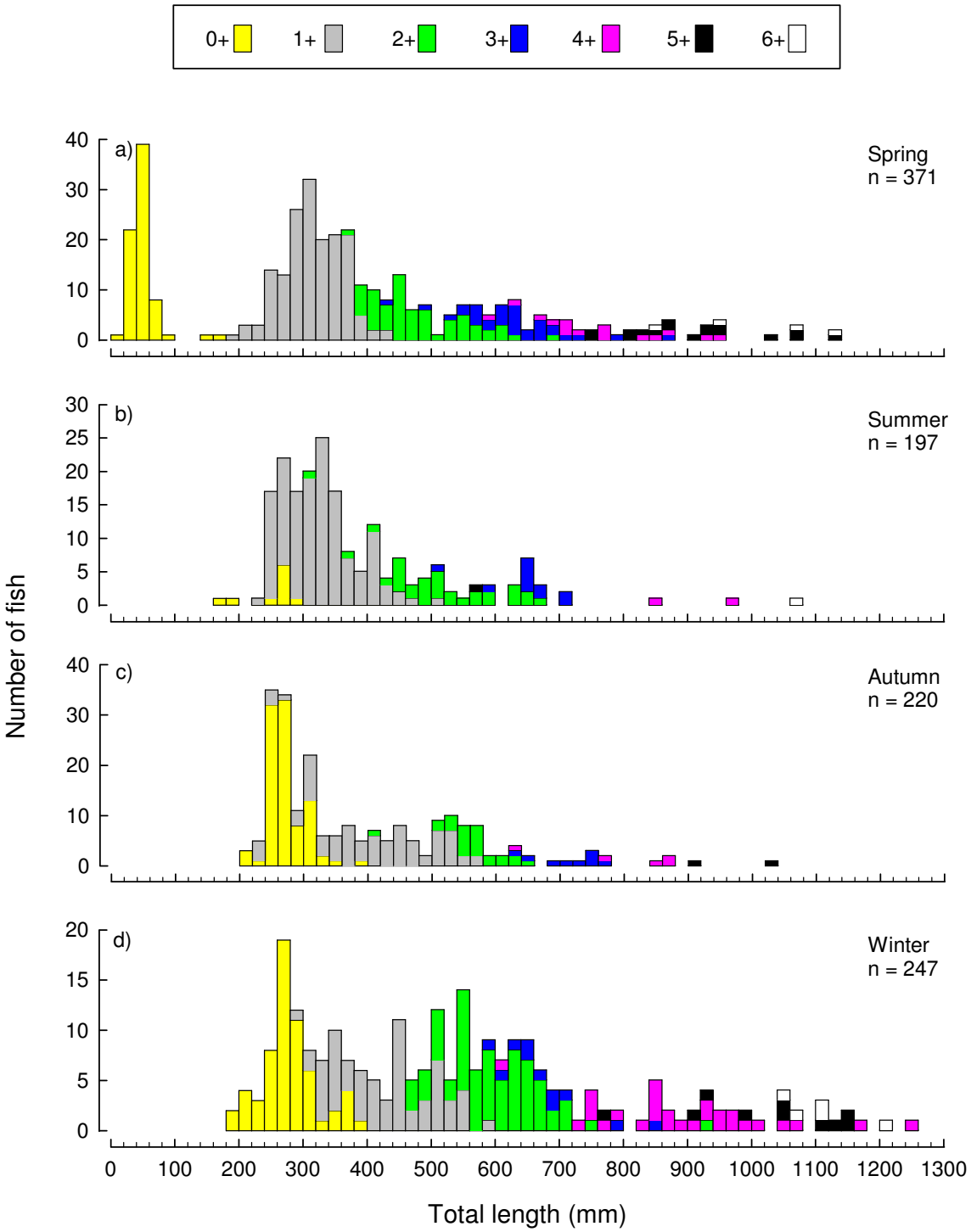

Figure 6.5. Length-frequency distributions of the different age classes of *Polydactylus macrochir* caught with seine and gill nets and by recreational fishers in nearshore waters in north-western Australia during a) spring, b) summer, c) autumn and d) winter.

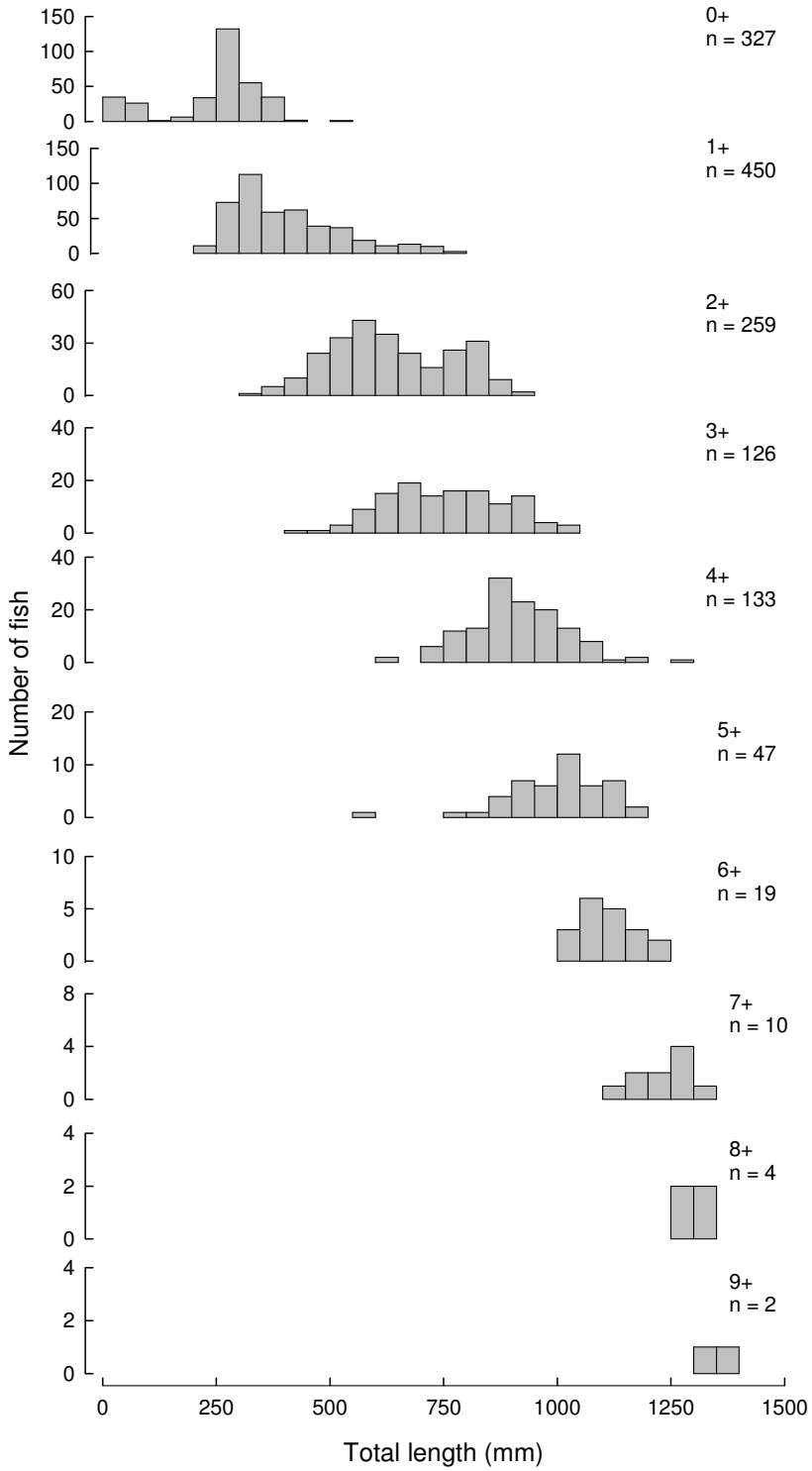

Figure 6.6. Length-frequency distributions of the different age classes of *Polydactylus macrochir* caught with seine and gill nets and by recreational and commercial fishers in nearshore waters of north-western Australia.

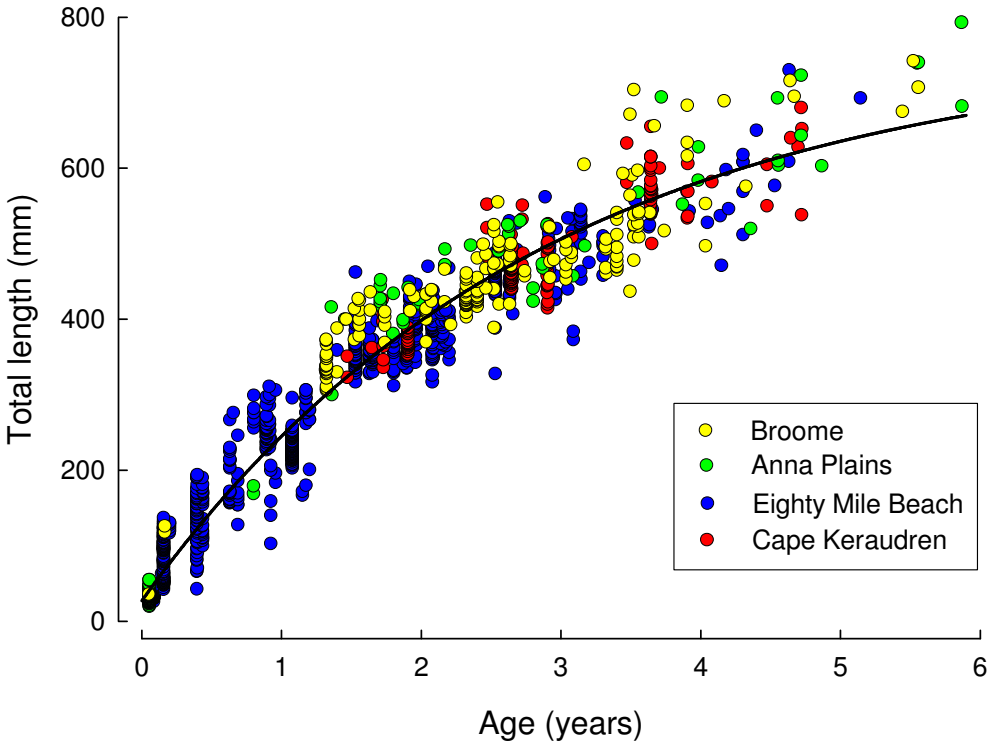

Figure 6.7. von Bertalanffy growth curve fitted to lengths at age of individuals of *Eleutheronema tetradactylum* collected from nearshore waters at Roebuck Bay, Anna Plains, Eighty Mile Beach and Cape Keraudren.

Table 6.1. Maximum length (L_{max}) and the parameters and their 95% confidence intervals for the von Bertalanffy growth equation fitted to the lengths at age of individuals of *Eleutheronema tetradactylum* and *Polydactylus macrochir*. L_∞ = asymptotic length, k = growth coefficient, t_0 = the hypothetical age at which fish would have zero length, R^2 = coefficient of determination, n = number of fish.

Species	L_{max} (mm)	L_∞ (mm)	k (years^{-1})	t_0 (years)	R^2	n
Eleutheronema tetradactylum	793	762	0.351	-0.103	0.967	1466
Upper 95% CI		786	0.370	-0.088		
Lower 95% CI		739	0.333	-0.118		
Polydactylus macrochir	1393	1587	0.170	-0.338	0.871	1377
Upper 95% CI		1709	0.192	-0.262		
Lower 95% CI		1466	0.148	-0.415		

von Bertalanffy growth curve likewise provided a good fit to the lengths at age of individuals of *P. macrochir* (**Table 6.1, Figure 6.8**). However, pairwise *t* tests revealed that the total lengths of *P. macrochir* between the ages of 1 and 4 were significantly longer (p<0.001) at Roebuck Bay than at the three other sampling regions, *i.e.* Derby, Anna Plains and Eighty Mile Beach. *Polydactylus macrochir* attained a greater maximum length and age than *E. tetradactylum*, *i.e.* 1393 vs 793 mm and 10 vs 6 years, respectively. The L_∞ was greater for *P. macrochir* than *E. tetradactylum, i.e.* 1587 *vs* 762 mm, whereas the reverse was true for the growth coefficient (k), *i.e.* 0.170 *vs* 0.351 years^{-1} (**Table 6.1, Figure 6.9**).

6.3.5. Length and age compositions of threadfin caught by various methods

The lengths of *E. tetradactylum* caught in research seine nets at Eighty Mile Beach lay largely between 26 and 250 mm, whereas those caught by research gill nets at the same location ranged predominantly from 210 to 550 mm (**Figure 6.10a, b**). The latter range is similar to that of fish caught by recreational anglers at Eighty Mile Beach (**Figure 6.10c**). The vast majority of the fish caught by recreational haul netting at Eighty Mile Beach and by commercial fishing at Anna Plains and Roebuck Bay exceeded 375 mm and included some fish with lengths in excess of 675 mm (**Figure 6.10d, e, f**).

The *E. tetradactylum* caught by research seine nets were mainly in their first year of life, whereas those taken by research gill nets belonged predominantly to 0+ to 4+ age

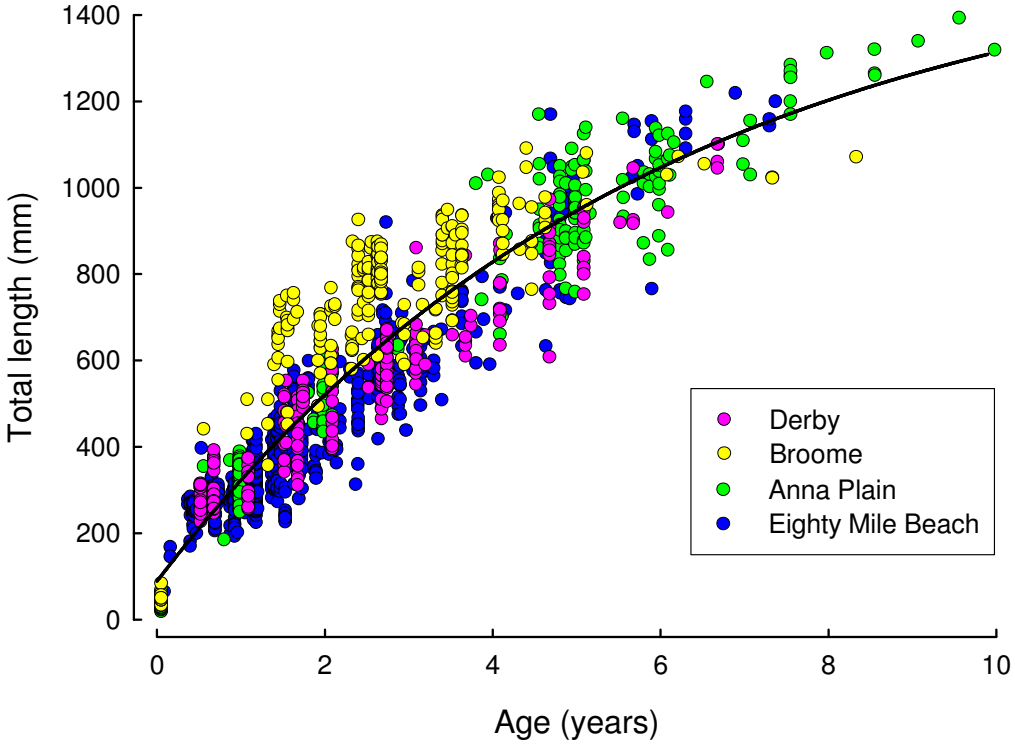

Figure 6.8. von Bertalanffy growth curve fitted to lengths at age of individuals of *Polydactylus macrochir* collected from nearshore waters at Derby, Roebuck Bay, Anna Plains and Eighty Mile Beach.

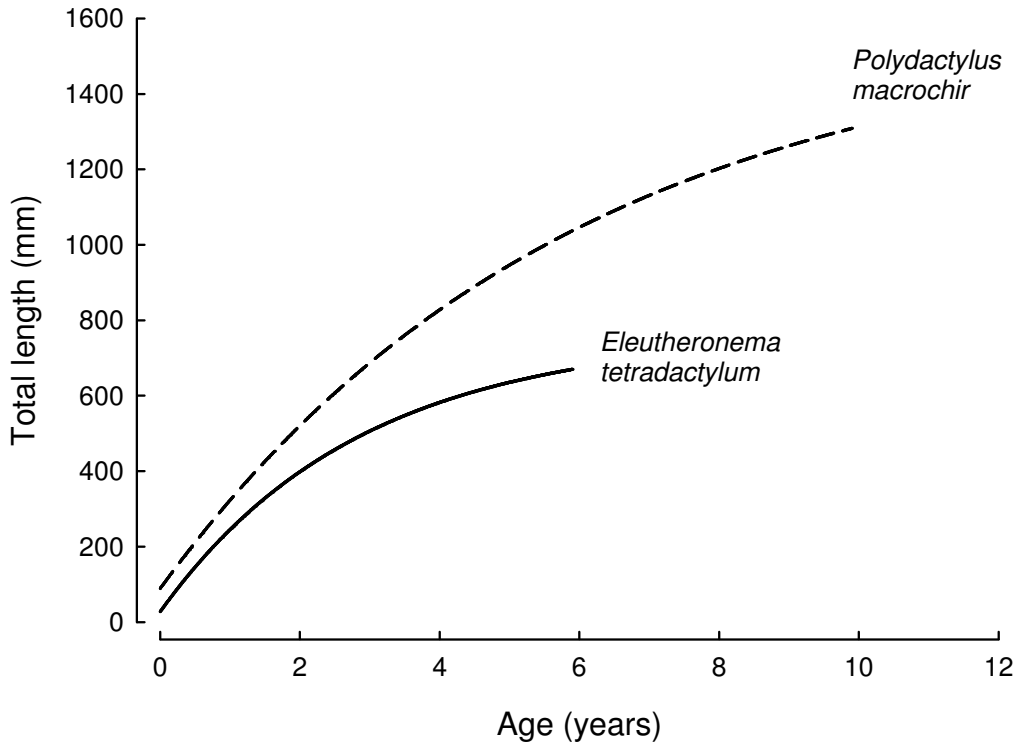

Figure 6.9. Comparison of von Bertalanffy growth curves fitted to lengths at ages of individuals of *Polydactylus macrochir* and *Eleutheronema tetradactylum*.

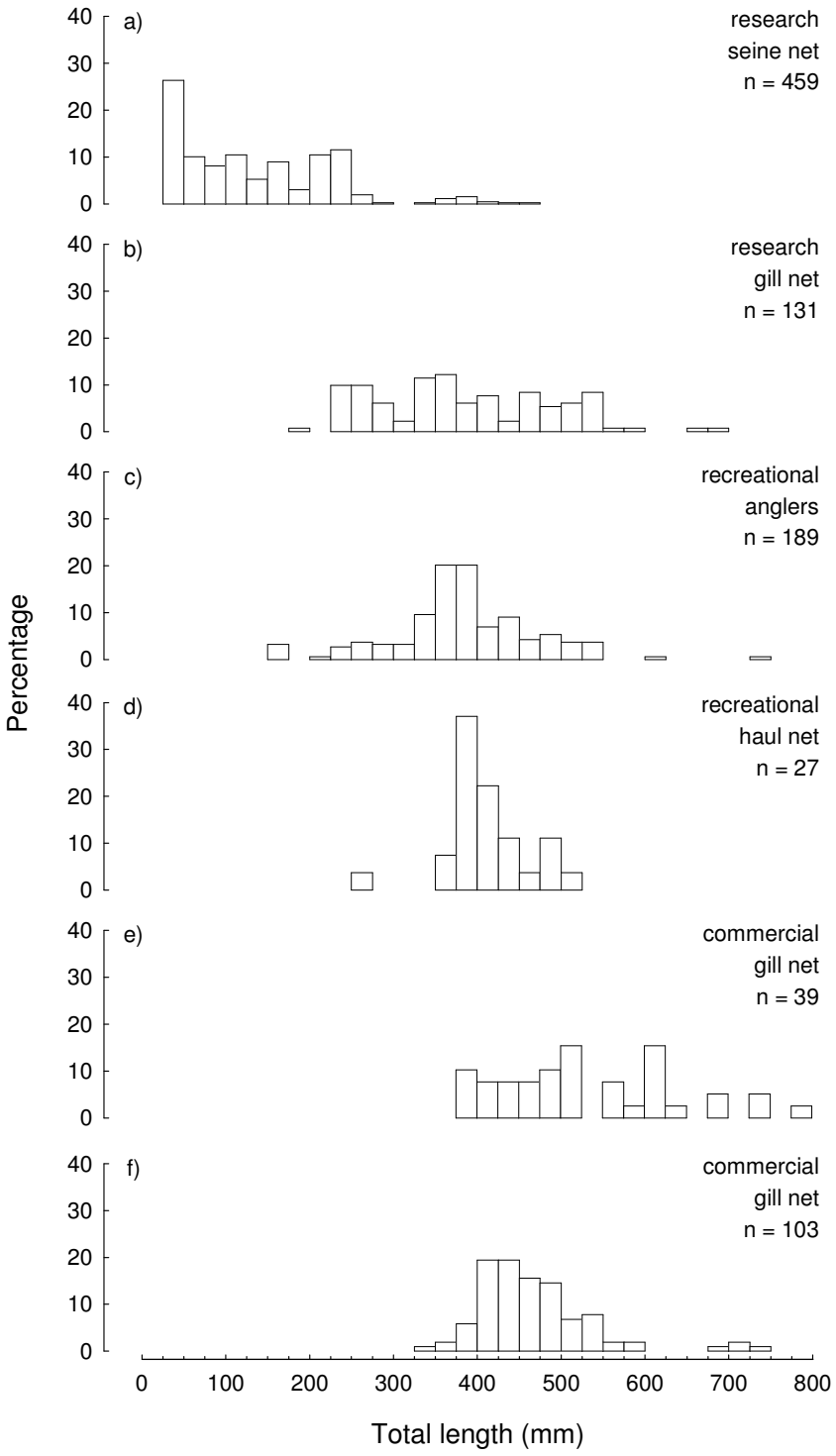

Figure 6.10. Length-frequency distributions for *Eleutheronema tetradactylum* caught at Eighty Mile Beach (a-d), Anna Plains (e) and Roebuck Bay (f) using different methods.

classes (**Figure 6.11a, b**). The fish caught by recreational anglers belonged predominantly to the 1+ and 2+ age classes (**Figure 6.11c**), while those taken by commercial gill nets, included all age classes from 1+ to 5+ (**Figure 6.11e, f**)

In contrast to the situation with *E. tetradactylum*, the length distributions of the *P. macrochir* caught using research seine and gill nets at Eighty Mile Beach did not differ markedly, with most fish obtained by these two methods lying between 200 and 550 mm (**Figure 6.12a, b**). The majority of fish caught by recreational anglers and haul netters at the same location lay between 500 and 1000 mm (**Figure 6.12c, d**). The catches obtained by commercial gill netting at Anna Plains (mesh size = 165 mm) and Roebuck Bay (mesh size = 140 mm) contained few fish < 550 mm and produced well defined modal length classes at 850 to 899 mm and 800 to 849 mm, respectively (**Figure 6.12e, f**).

The *P. macrochir* caught by seine netting and gill netting were predominantly in their first three years of life, whereas those obtained by recreational anglers were mainly in their third to fifth years of life (*i.e.* 2+, 3+ and $+ age classes) and included fish in their ninth and tenth years of life (**Figure 6.13a, b, c**). Recreational haul netting tended to catch younger fish than recreational angling and did not yield fish older than five years (*cf* **Figure 6.13c, d**). The ages of the fish caught by commercial gill netting at Anna Plains and Roebuck Bay differed markedly, with the modal age class being 4+ at the former locality and 2+ at the latter locality, presumably reflecting, at least in part, a larger mesh size, *i.e.* 165 *vs* 140 mm (**Figure 6.13e, f**).

6.3.6. Estimates of total and natural mortality

The values derived for total mortality, *Z*, for *E. tetradactylum,* using the regression equation refitted to Hoenig's (1983) fish data, relative abundance (catch curve) analysis (**Figure 6.14a**) and simulation (based on only nine of 121 fish in the descending limb of the recreational sample being ≥ 4 years) ranged from 0.73 to 1.37 year^{-1} (**Table 6.2, Figure 6.15a**). These values were thus all greater than the 0.68 derived for natural mortality, *M*, using the refitted equation of Pauly (1980). The use of the Bayesian method of Hall *et al*. (2004), which combines the separate likelihood estimates of *Z* and ensures that *M* must be < *Z*, yielded values of 1.31 and 0.61 for *Z* and *M*, respectively (**Table 6.2,**

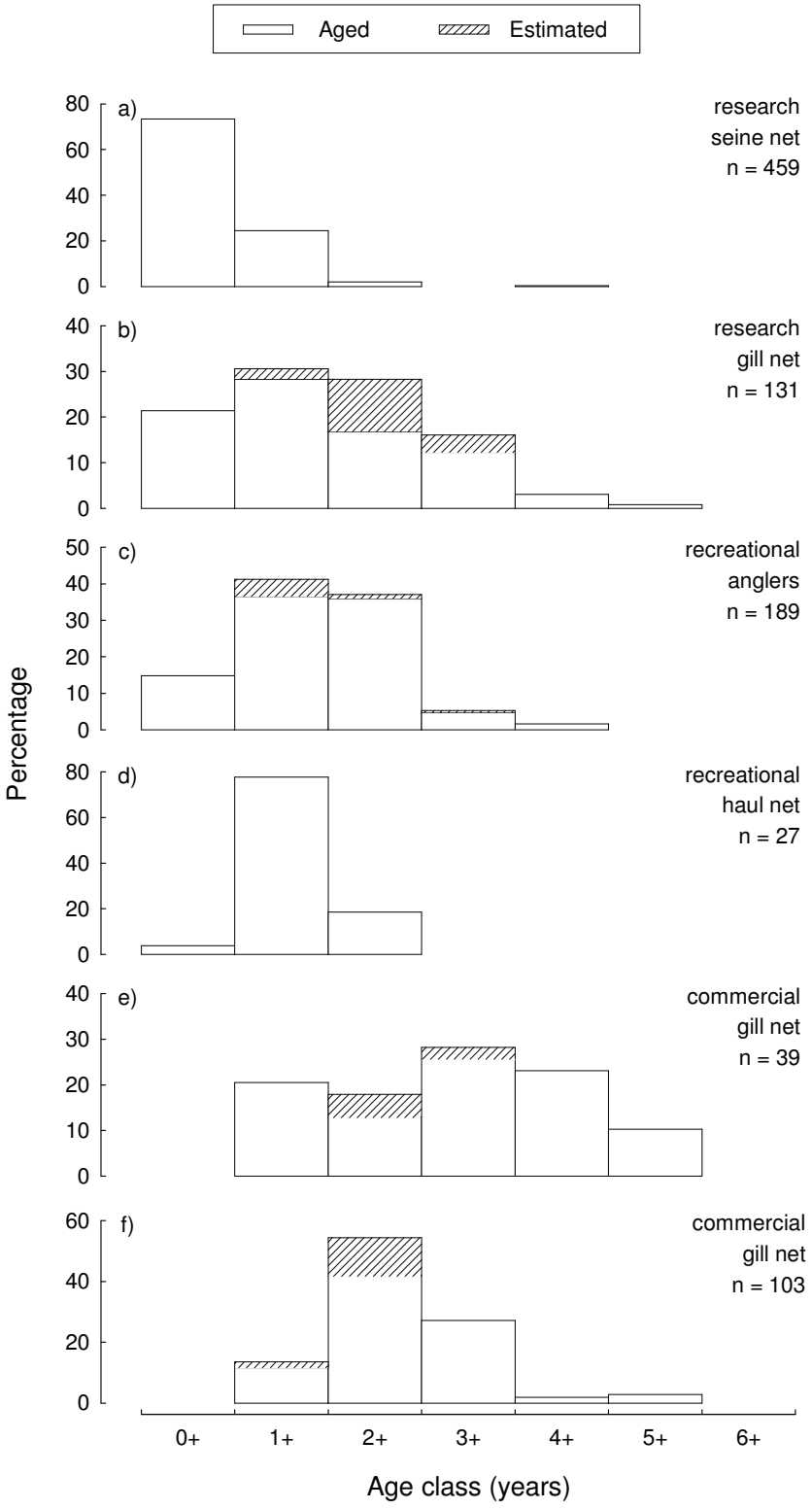

Figure 6.11. Age-frequency distributions for *Eleutheronema tetradactylum* caught at Eighty Mile Beach (a-d), Anna Plains (e) and Roebuck Bay (f) using different methods.

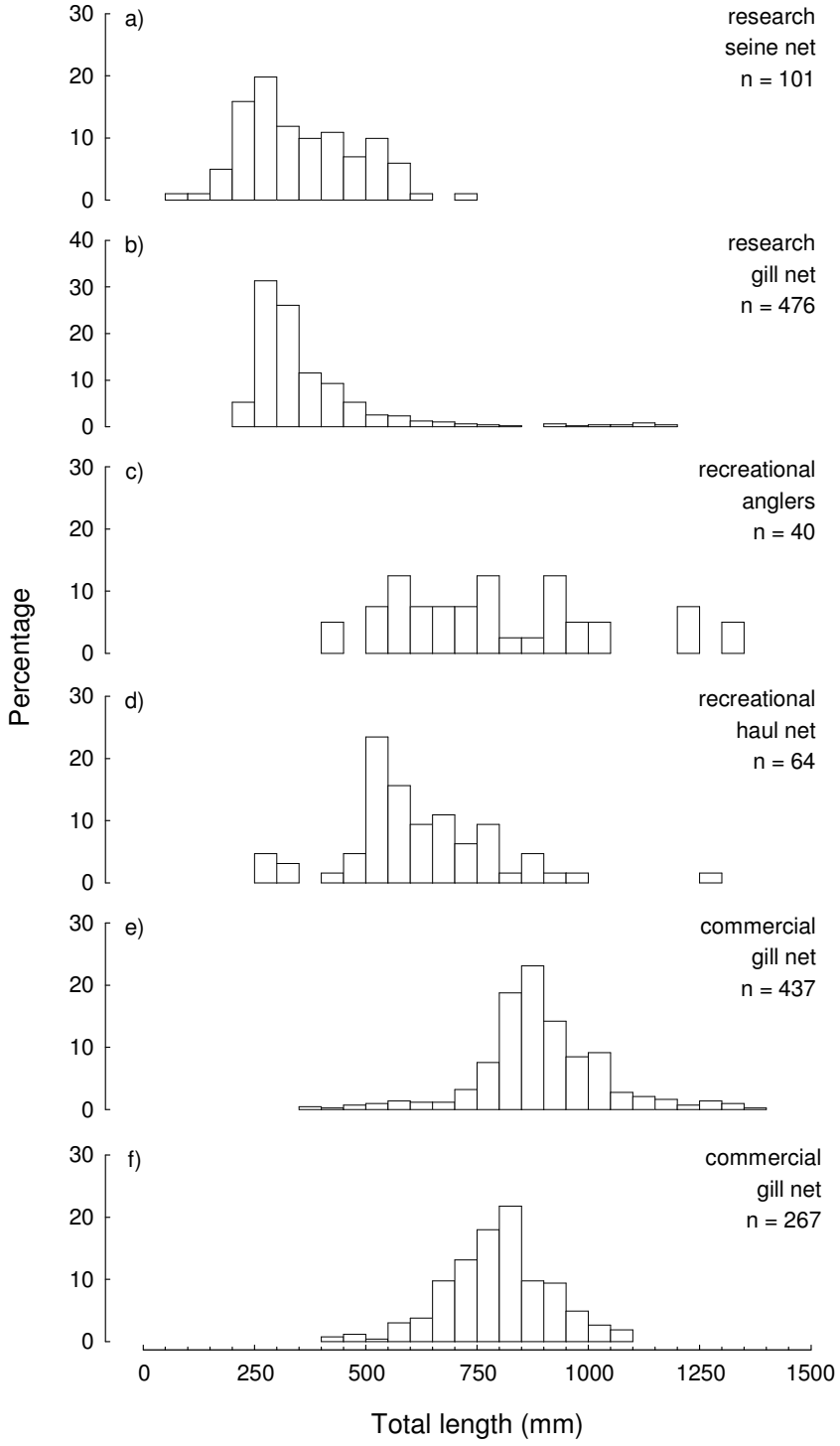

Figure 6.12. Length-frequency distributions for *Polydactylus macrochir* caught at Eighty Mile Beach (a-d), Anna Plains (e) and Roebuck Bay (f) using different methods.

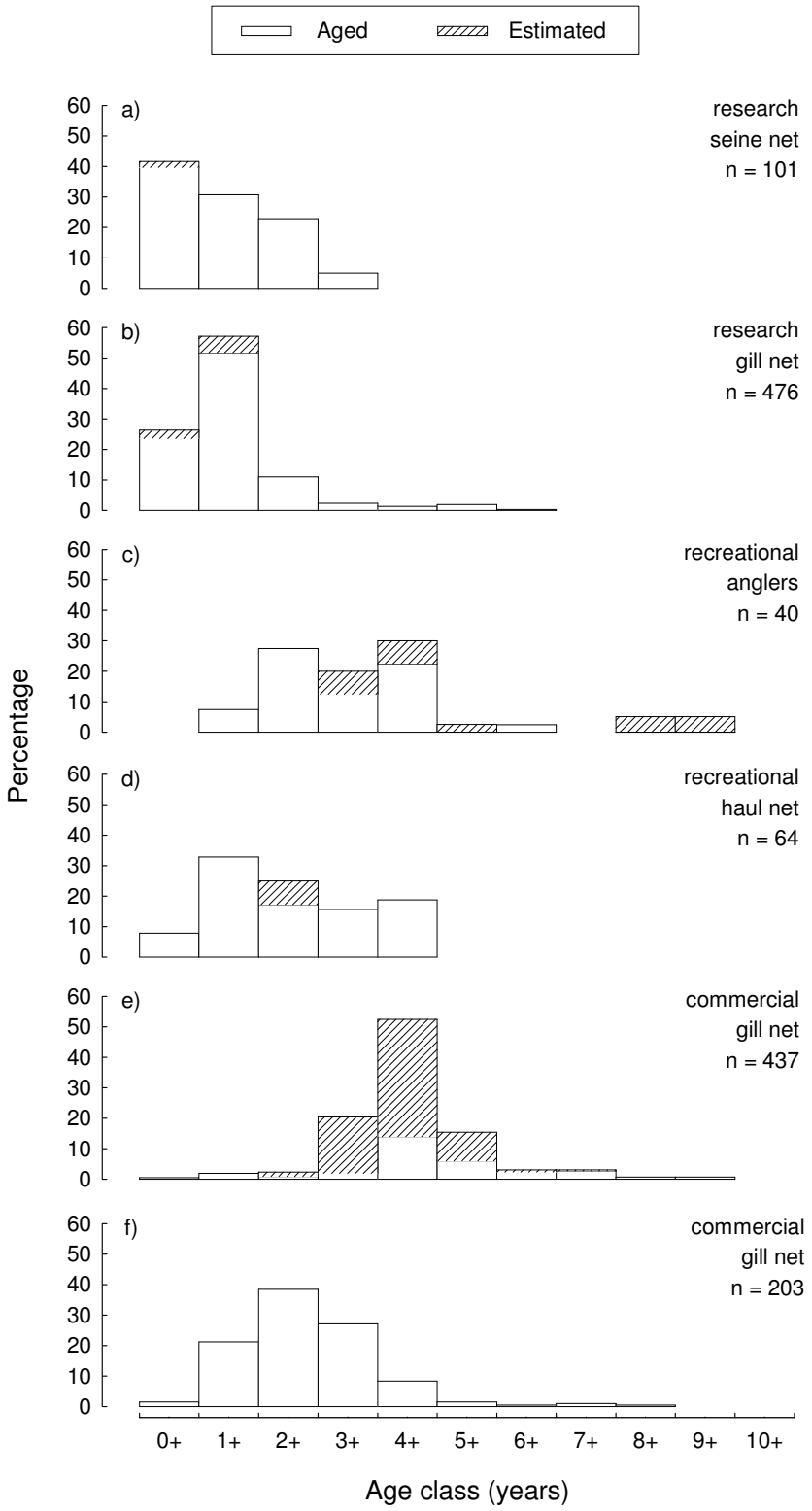

Figure 6.13. Age-frequency distributions for *Polydactylus macrochir* caught at Eighty Mile Beach (a-d), Anna Plains (e) and Roebuck Bay (f) using different methods.

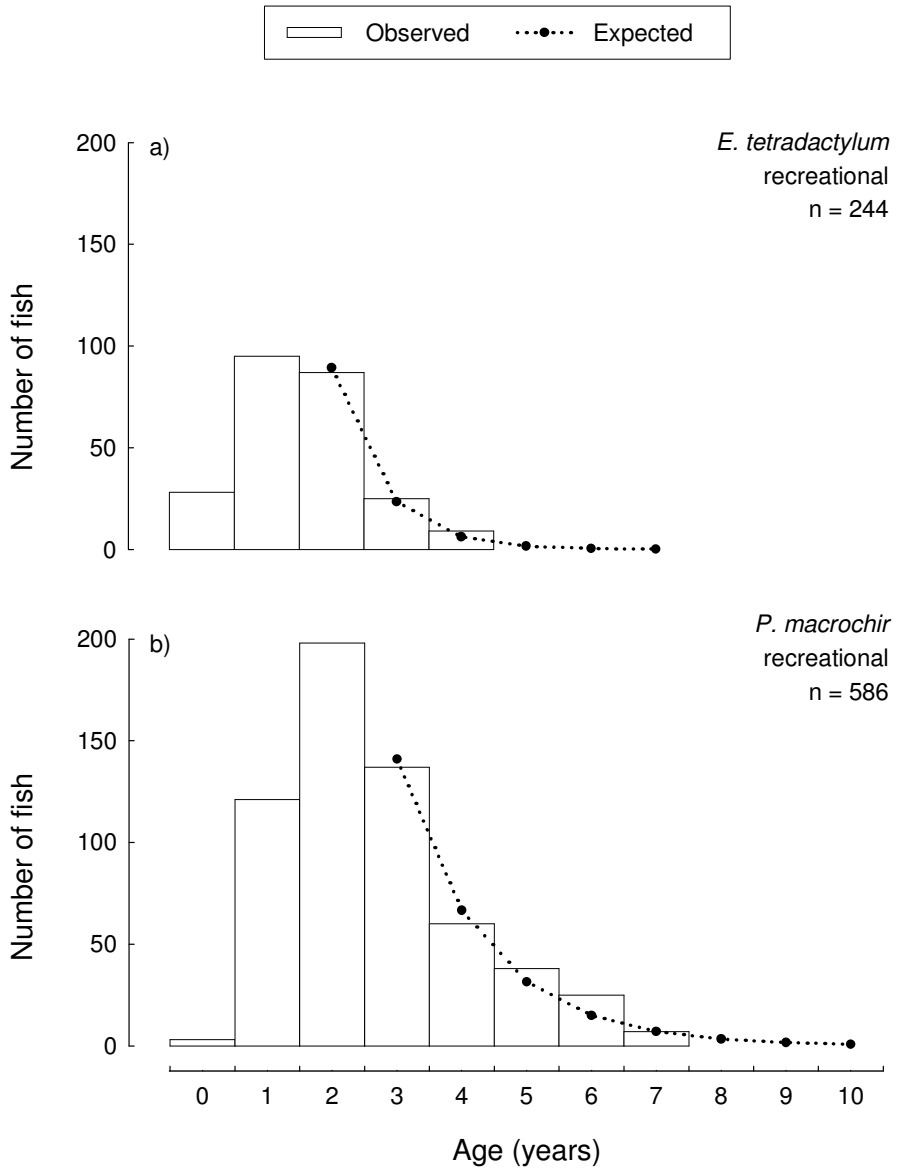

Figure 6.14. Relative abundance (catch curve) analyses were used to fit lines to the observed frequency of abundance of fish in each year class of a) *Eleutheronema tetradactylum* and b) *Polydactylus macrochir* and assuming that recruitment is constant. Abundance data for *E. tetradactylum* is from recreational catches aged from random samples collected between Karratha and Broome during the study and for *P. macrochir* relates to ages back transformed from the lengths of fish released during a recreational tagging study.

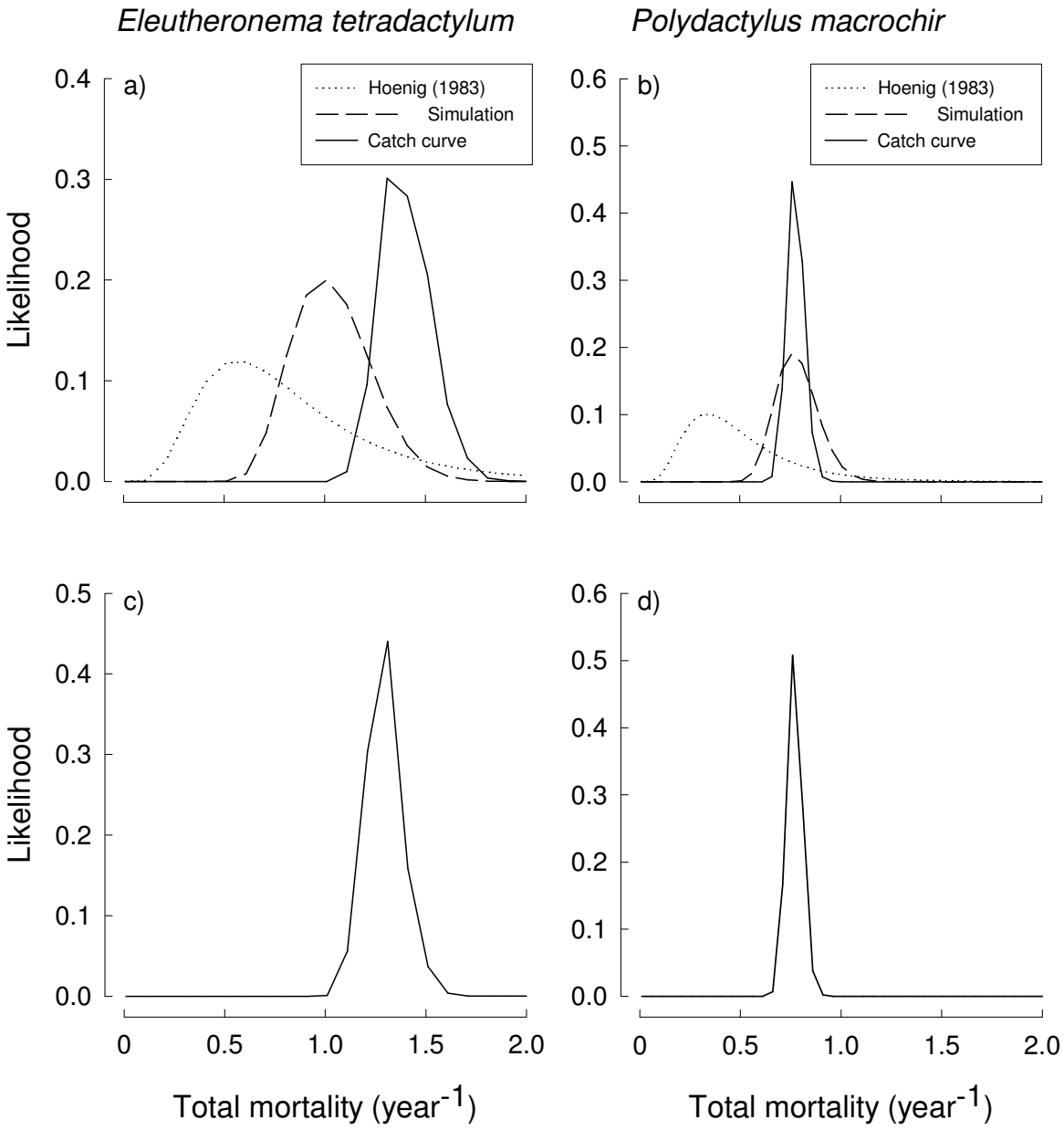

Figure 6.15. Estimated likelihood functions for total mortality *Z* of (a) *Eleutheronema tetradactylum* and (b) *Polydactylus macrochir* derived using Hoenig's (1983) regression equation for fish, relative abundance (catch curve) analysis, and a simulation method based on the number of fish in the samples that exceeded specified ages and the sizes of the samples. (c,d) Combined posterior probability distributions for *Z* for (c) *E. tetradactylum* and (d) *P. macrochir* derived from the separate likelihood functions shown in (a) and (b).

Table 6.2. Mortality (year^{-1}) of *Eleutheronema tetradactylum* and *Polydactylus macrochir* in north-western Australia calculated using different life history models, simulation based on the number of fish in the sample with ages in excess of a specified age or relative abundance analyses. *M* = natural mortality, *Z* = total mortality, *F* = fishing mortality.

Method of analysis	*M* or *Z* or *F* (year^{-1})	Estimate	Lower 95%	Upper 95%
Eleutheronema tetradactylum				
Refitted Hoenig (1983)	*Z*	0.73	0.26	2.05
Relative abundance - recreational anglers	*Z*	1.37	1.14	1.62
Simulation based on maximum age	*Z*	1.08	0.75	1.49
Combined Bayesian estimate of *Z*	***Z***	**1.31**	**1.11**	**1.51**
Refitted Pauly (1980)	*M*	0.68	0.22	2.11
Combined Bayesian estimate of *M*	***M***	**0.61**	**0.21**	**1.31**
Monte Carlo estimate of *F*	***F***	**0.70**	**0.00**	**1.11**
Polydactylus macrochir				
Refitted Hoenig (1983)	*Z*	0.44	0.16	1.21
Relative abundance - tagging release data	*Z*	0.78	0.67	0.85
Simulation based on maximum age	*Z*	0.80	0.62	1.02
Combined Bayesian estimate of *Z*	***Z***	**0.76**	**0.71**	**0.86**
Refitted Pauly (1980)	*M*	0.35	0.11	1.07
Combined Bayesian estimate of *M*	***M***	**0.31**	**0.11**	**0.71**
Monte Carlo estimate of *F*	***F***	**0.45**	**0.05**	**0.65**

Figure 6.15c, 6.16). The value for fishing mortality, *F*, was 0.70, but had very wide confidence limits (**Table 6.2**).

As with *E. tetradactylum*, the values derived for *Z*, for *P. macrochir,* using the equation of Hoenig (1983), relative abundance analysis (**Figure 6.14b**) and simulation (based on seven of 267 fish in the descending limb of the recreational sample being ≥ 7 years), *i.e.* 0.44 to 0.80 year^{-1}, exceeded the value of 0.35 year^{-1} derived for *M* using the refitted equation of Pauly (1980) (**Table 6.2, Figure 6.15b**). The Bayesian method of Hall *et al*. (2004) yielded values of 0.76 and 0.31 year^{-1} for *Z* and *M*, respectively (**Table 6.2,**

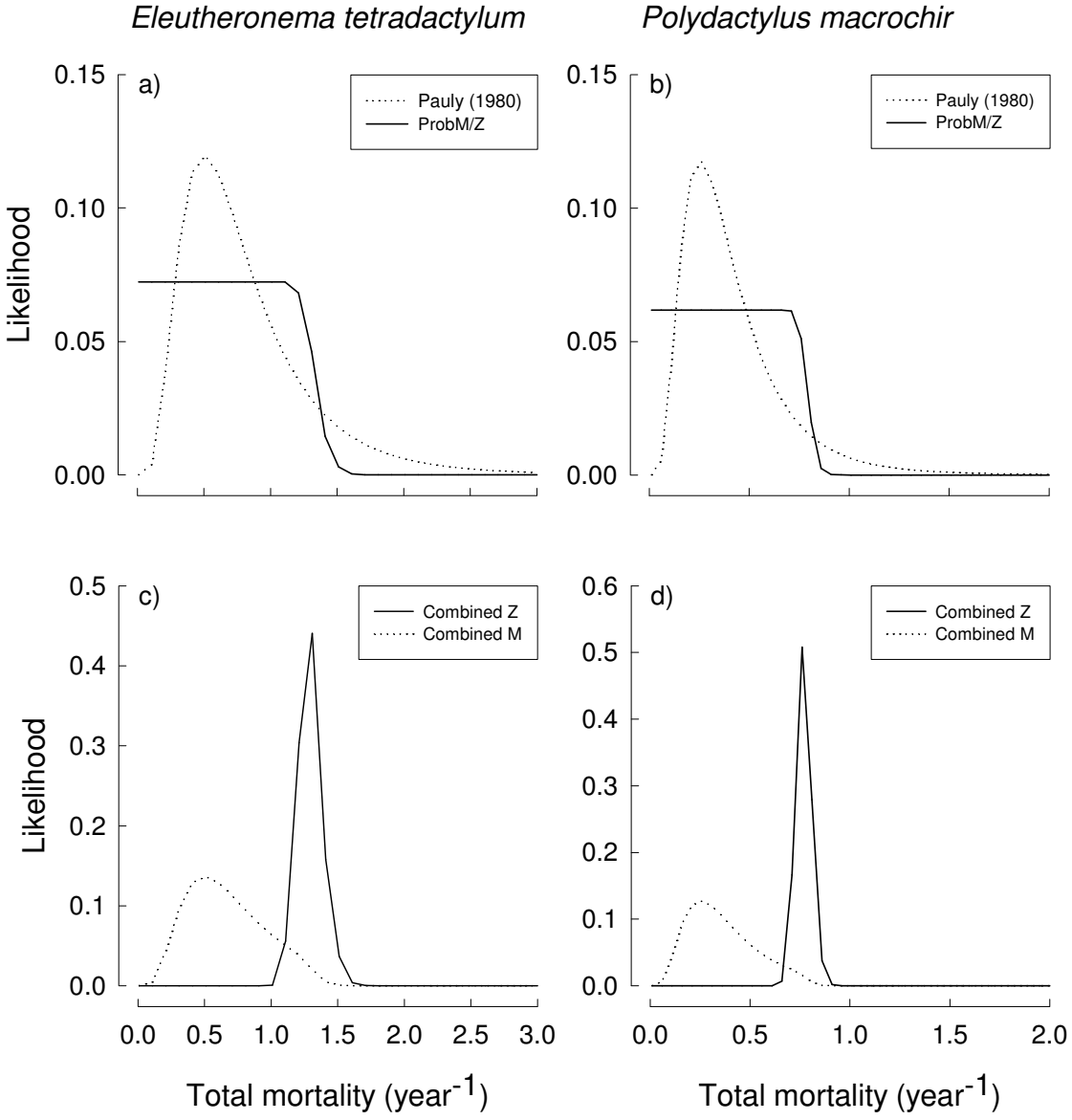

Figure 6.16. Likelihood functions for natural mortality *M* for (a) *Eleutheronema tetradactylum* and (b) *Polydactylus macrochir* from Pauly's (1980) equation and the likelihood function for *M* assuming that it is less than the combined estimate for *Z* and the combined posterior probability distributions for *Z* and *M* for (c) *E. tetradactylum* and (d) *P. macrochir.*

Figure 6.15d, 6.16). The value for fishing mortality, *F*, was 0.45, but, as with *E. tetradactylum*, had very wide confidence limits (**Table 6.2**).

6.3.7. Yield per recruit, spawning potential ratio and spawning biomass per recruit

The yield per recruit analysis (YPR) for *E. tetradactylum*, calculated using a knife edge recruitment to the fishery of 2 years, indicated that, as *F* increased from 0 to 1.5 year^{-1}, the YPR also continued to increase (**Figure 6.17a**). The predicted YPR and associated 95% confidence intervals for *E. tetradactylum* at the estimated current level of *F* of 0.7 year^{-1} and age of recruitment to the fishery of 2 years, is 0.12 kg recruit^{-1} (0.00 – 0.42 kg recruit^{-1}) (**Table 6.3**). As YPR continued to increase, it was not possible to determine a value for F_{max} for *E. tetradactylum*. The $F_{0.1}$ value of 0.57 year^{-1} calculated for *E. tetradactylum* is lower than the current level of *F* estimated for this species (**Tables 6.2, 6.3**). Although YPR also increases with *F* if the age of recruitment to the fishery was 3 years, if it was 1 year, the YPR begins to decline at levels of *F* exceeding *ca* 0.4 year^{-1} (**Figure 6.17a**). The current ages of recruitment to the exploited stocks of *P. macrochir* at Roebuck Bay and Anna Plains are 3 and 4 years, respectively. At these recruitment ages, the YPR for *P. macrochir* at Roebuck Bay began to decline at levels of *F* greater than *ca* 0.6 year^{-1} however that at Anna Plains continued to increase (**Table 6.2, Figure 6.18a, b**). The estimated YPR for the Roebuck Bay and Anna Plains stocks of *P. macrochir*, at the estimated current level of *F* of 0.45 year^{-1}, and recruitment ages of 3 and 4 years, were 0.84 and 0.88 kg recruit^{-1}, respectively (**Table 6.4**).

The value of F_{max} (0.59 year^{-1}) calculated for the Roebuck Bay stock of *P. macrochir,* with an age of recruitment to the fishery of 3 years, exceeded the estimated current level of *F* of 0.45 year^{-1}, and that for $F_{0.1}$ (0.25 year^{-1}) was much less (**Tables 6.2, 6.4**). Although YPR continued to increase with *F* if the age of recruitment to the fishery was 4 years, it began to decline at levels of *F* exceeding *ca* 0.35 year^{-1} if the age of recruitment was only 2 years (**Figure 6.18a**).

As the level of YPR for the Anna Plains stock, which had an age of recruitment to the fishery of 4 years, continued to increase with *F*, it was not possible to determine a value for F_{max} for this stock. The value of $F_{0.1}$ (0.31 year^{-1}) calculated for the Anna Plains

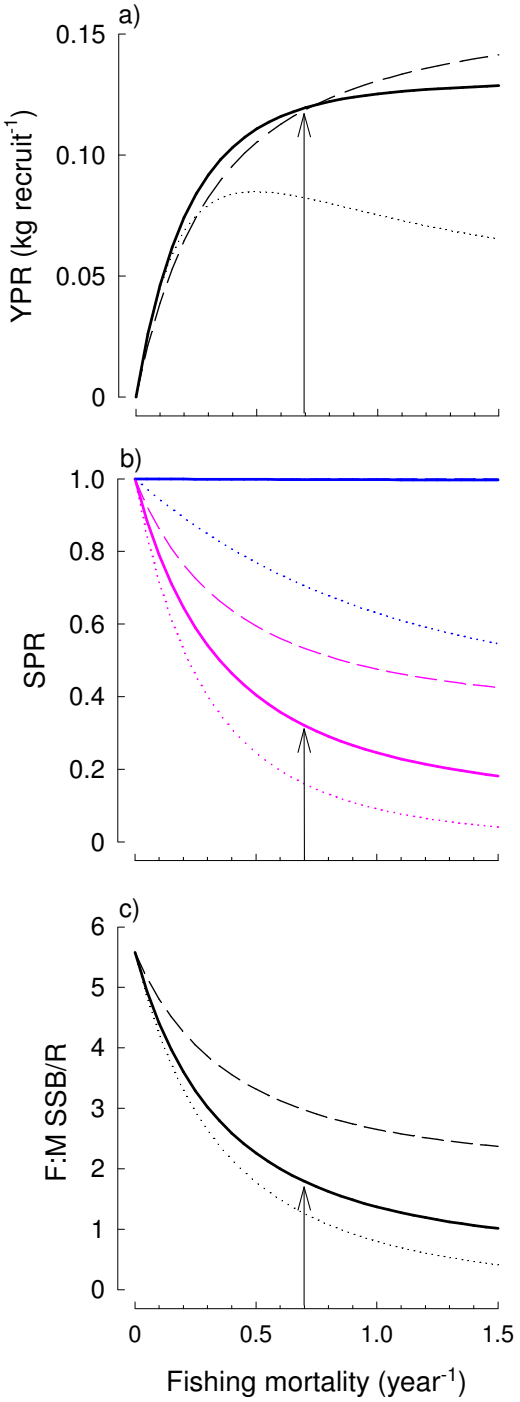

Figure 6.17. Effect, for *Eleutheronema tetradactylum*, of different levels of fishing mortality (year^{-1}) and at different ages of recruitment to the exploited stock on the yield per recruit (a), spawning potential ratio, for male (blue) and female (pink) spawning stock biomass (b) and on the ratio of female to male spawning stock biomass (c). The dotted, solid and dashed lines correspond to ages at full recruitment of 1, 2 & 3, respectively. The arrows indicate the current level of fishing mortality estimated for *E. tetradactylum* of 0.7 year^{-1}.

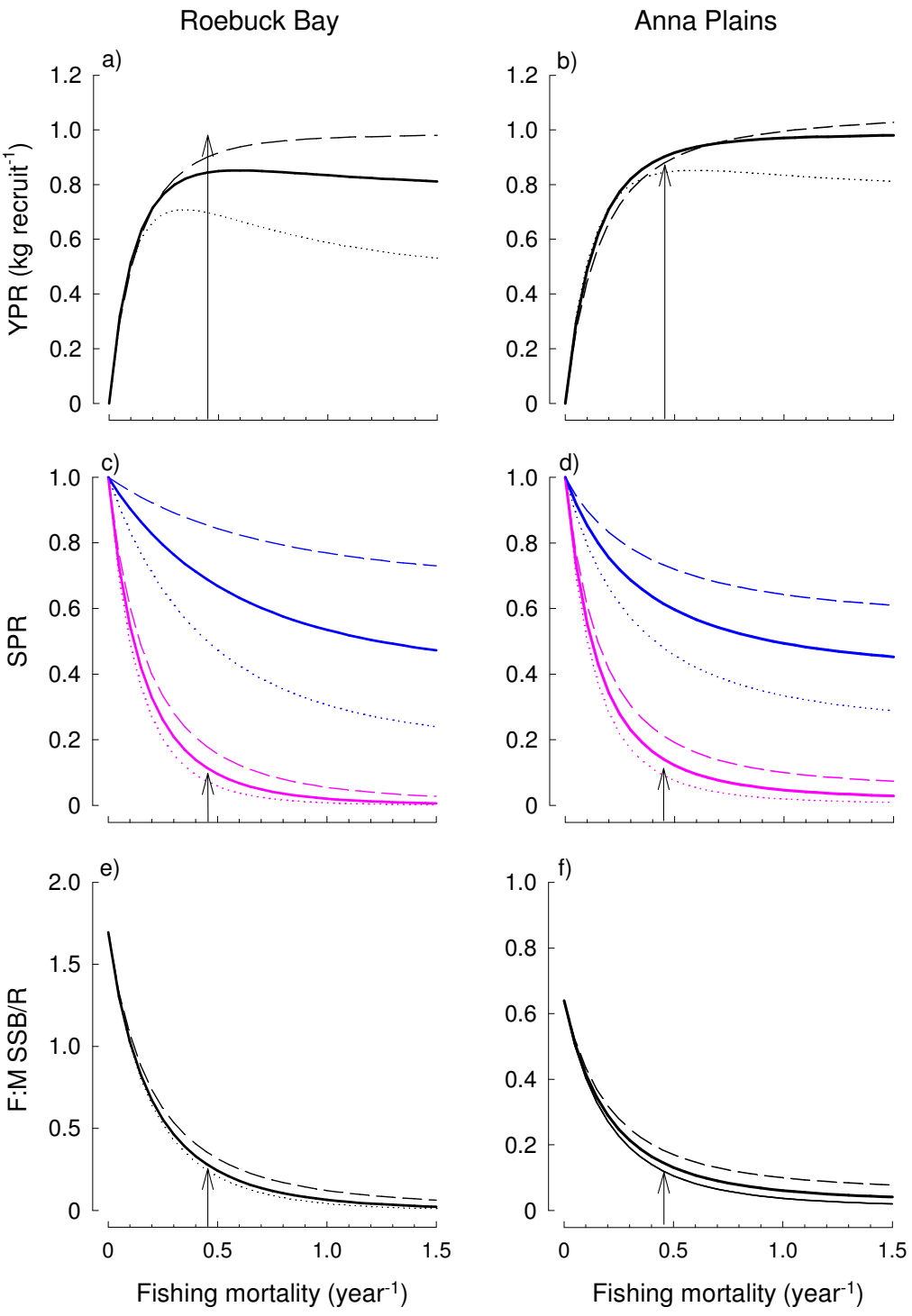

Figure 6.18. Effect, for stocks of *Polydactylus macrochir* at Roebuck Bay and Anna Plains, of different levels of fishing mortality (year^{-1}) and at different ages of recruitment to the exploited stock on the yield per recruit (a, b), spawning potential ratio, for male (blue) and female (pink) spawning stock biomass (c, d) and on the ratio of female to male spawning stock biomass (e, f). The dotted, solid and dashed lines correspond to ages at full recruitment of 2, 3 & 4 and 3, 4 & 5 for the Roebuck Bay and Anna Plains stocks of *P. macrochir*, respectively. The arrows indicate the current level of fishing mortality estimated for *P. macrochir* of 0.45 year^{-1}.

Table 6.3. Estimates of the current level of yield per recruit (YPR), $F_{0.1}$ and the current levels of total spawning stock biomass per recruit (SSB/R) and spawning potential ratio (SPR) for females, males and females and males combined, for *Eleutheronema tetradactylum*, calculated using 2 years as the age at full recruitment to the fishery. N.B. It was not possible to determine F_{max} for *E. tetradactylum*.

Method of analysis	Estimate	Lower 95%	Upper 95%
Monte Carlo estimate of YPR (kg recruit^{-1})	0.12	0.00	0.42
$F_{0.1}$ (year^{-1})	0.57		
Monte Carlo estimate of SSB/R	0.37	0.13	0.79
SPR (males)	1.00	0.99	1.00
SPR (females)	0.36	0.06	1.00
SPR (males & females)	0.46	0.09	1.00

Table 6.4. Estimates of the current level of yield per recruit (YPR), F_{max}, $F_{0.1}$ and the current levels of total spawning stock biomass per recruit (SSB/R) and spawning potential ratio (SPR) for females, males and females and males combined, for stocks of *Polydactylus macrochir* at Roebuck Bay and Anna Plains, calculated using 3 and 4 years as the ages at full recruitment to the fishery for the Roebuck Bay and Anna Plains stocks, respectively. N.B. It was not possible to determine F_{max} for the stock of *P. macrochir* at Anna Plains.

Method of analysis	Estimate	Lower 95%	Upper 95%
Roebuck Bay			
Monte Carlo estimate of YPR (kg recruit^{-1})	0.84	0.02	2.22
F_{max} (year^{-1})	0.59		
$F_{0.1}$ (year^{-1})	0.25		
Monte Carlo estimate of SSB/R	3.13	1.07	5.81
SPR (males)	0.71	0.53	0.97
SPR (females)	0.13	0.02	0.83
SPR (males & females)	0.35	0.07	0.95
Anna Plains			
Monte Carlo estimate of YPR (kg recruit^{-1})	0.88	0.02	2.90
$F_{0.1}$ (year^{-1})	0.31		
Monte Carlo estimate of SSB/R	4.18	1.12	8.85
SPR (males)	0.64	0.33	0.98
SPR (females)	0.16	0.02	0.87
SPR (males & females)	0.45	0.11	0.97

stock of *P. macrochir,* was below the estimated current level of *F* for this species (**Table 6.2, 6.4**). Although YPR for *P. macrochir* at Anna Plains also continued to increase with *F* if the age of recruitment to the fishery increased to 5 years, it began to decline at levels of *F* exceeding *ca* 0.6 year^{-1} if the age of recruitment was 3 years (**Figure 6.18a**).

The spawning potential ratio (SPR) of male *E. tetradactylum* decreased with increasing levels of *F* only when the age at full recruitment to the exploited stock was 1 year. At the recruitment ages of 2 and 3 years, there was no reduction in the SPR (**Figure 6.17b**). In contrast, irrespective of recruitment age, the SPR of female *E. tetradactylum* decreased with increasing levels of *F* and was less than that of males (**Figure 6.17b**). The rate at which female SPR declined varied with recruitment age and was greatest for age 1 and least for age 3. The current estimated SPRs for male and female *E. tetradactylum* are 1.00 and 0.36, respectively (**Table 6.3, Figure 6.17b**).

Regardless of the age at recruitment, an increase in *F* for *P. macrochir* resulted in the spawning potential ratio (SPR) decreasing far more rapidly for its females than its males at both Roebuck Bay and Anna Plains (**Figures 6.18c, d**). In the case of both female and males, the rate at which SPR is predicted to decline decreases substantially as the age at recruitment increases from 2 to 4 years at Roebuck Bay and from 3 to 5 years at Anna Plains **(Figures 6.18c, d)**. The current estimated SPRs for male and female *P. macrochir* at Roebuck Bay and Anna Plains are 0.71 and 0.13 and 0.64 and 0.16, respectively (**Table 6.4**).

For *E. tetradactylum* and the stocks of *P. macrochir* at Roebuck Bay and Anna Plains*,* as *F* increases from 0 year^{-1}, the ratio of female to male spawning stock biomass per recruit (SSB/R) declines exponentially from initial values of *ca* 5.58 1.69 and 0.64, respectively (**Figures 6.17c, 6.18e,f**). The current estimated ratios of female to male SSB/R for *E. tetradactylum* and the two stocks of *P. macrochir* are 1.79, 0.28 and 0.15, respectively (**Figure 6.17c, 6.18e,f**).

6.4. Discussion

6.4.1. Age and growth

The trends exhibited by the mean monthly marginal increments demonstrated that a single opaque zone is formed annually in the otoliths of both *Eleutheronema tetradactylum* and *Polydactylus macrochir* and thus the number of opaque zones in otoliths could be used to age each species. In both species, the opaque zones were formed during winter, presumably reflecting slower growth in that season, and become fully delineated by October or November. The tendency for the opaque zones to become delineated slightly earlier in the younger age classes presumably reflects the rapid growth rates of these fish and parallels the situation observed in a number of other fish species (*i.e.* Fairclough *et al*., 2000; Coulson *et al*., 2005).

Although *E. tetradactylum* and *P. macrochir* both grow relatively rapidly early in life, attaining lengths of *ca* 400 mm by the end of their second year of life, the latter species subsequently grows more rapidly, which is reflected in asymptotic lengths of 1590 *vs* 760 mm and maximum lengths of *ca* 1400 *vs* 800 mm. *Polydactylus macrochir* also lives far longer than *E. tetradactylum* in north-western Australia, with several of its individuals caught during this study being six to ten years in age, whereas none of the latter species exceeded six years in age.

The rapid early growth rates exhibited by these two threadfin species parallels that reported for a number of other polynemids including *Leptomelanosoma indicum* (Kagwade, 1973), *Pentanemus quinquarius* (Longhurst, 1965), *Polydactylus mullani* (Kagwade, 1971; Prasad *et al*., 2005) and *Polydactylus octonemus* (Dentzau & Chittenden, 1990). In contrast, the West African polynemid *Galeoides decadactylus* has a slower growth rate, reaching total lengths of only *ca* 110 mm at the end of its first year of life and taking four to six years to reach lengths of *ca* 350 mm (Longhurst, 1961; Abohweyere, 1989).

The parameters derived for the von Bertalanffy growth curve for *E. tetradactylum* in north-western Australia are similar to those derived for this species in eastern Queensland by Stanger (1974), who fitted the curve to the lengths of fish aged three and below (**Table 6.5**). The maximum length and age of *E. tetradactylum* recorded during this

Table 6.5. Comparison of maximum age (A_{max}), maximum length (L_{max}) and the parameters for the von Bertalanffy growth equations for *Eleutheronema tetradactylum* and *Polydactylus macrochir* from studies from different Australian regions. L_∞ = asymptotic length, k = growth coefficient, t_0 = the hypothetical age at which fish would have zero length, n = number of fish. Study regions: North-western Australia (Present study), Gulf of Carpentaria (Garrett, 1992; Bibby & McPherson, 1997), eastern Queensland (Stanger, 1974; Russell, 1988), southern Queensland (Halliday *et al*., submitted). * = length recorded as fork length, estimated total lengths are given in parentheses. na = not aged. s = Schnute growth model fitted.

Region - Study	A_{max} (y)	L_{max} (mm)	L_∞ (mm)	k (years^{-1})	t_0 (years)	n
Eleutheronema tetradactylum						
Present study	6	793	762	0.351	-0.103	1466
Stanger, 1974	6	740	662* (790)	0.260	-0.750	66
Russell, 1988	na	650	-	-	-	1633
Bibby & McPherson, 1997	7	880* (1050)	s	s	s	195
Polydactylus macrochir						
Present study	10	1393	1587	0.170	-0.338	1377
Garrett, 1992	14	1065* (1280)	-	-	-	740
Bibby & McPherson, 1997	14	1365* (1625)	s	s	s	714
Russell, 1988	na	1200* (1450)	-	-	-	254
Halliday *et al.,* submitted	19	1270* (1500)	-	-	-	716

study of 793 mm and *ca* 7 years is similar to those recorded in eastern Australia (Stanger, 1974; Russell, 1988) but less than the *ca* 1050 mm and 7 years recorded in the Gulf of Carpentaria by Bibby & McPherson (1997) **(Table 6.5)**. *Eleutheronema tetradactylum* attains a far greater length in Indian waters than along the coast of north-western Australia, *i.e.* 1800-2000 *vs ca* 800 mm (Gopalakrishnan, 1972; Krishnamurthy & Jeyaseelan, 1981; Feltes, 1999). Although recreational fishing records suggest that *E. tetradactylum* in Australian waters attain a far greater weight than that recorded during this study, *i.e. ca* 15 kg *vs* 6 kg (Anon, 2006a), the confusion surrounding the identification of threadfin species and the interchangeable nature of common names makes it likely that this and other similar records are erroneous and probably refer to the larger *P. macrochir*.

Although the pattens of growth for *P. macrochir* from Derby, Anna Plains and Eighty Mile Beach were remarkably similar, the early growth of *P. macrochir* at Roebuck Bay was more rapid than at the other locations. The differences in growth presumably reflect differences among the locations in various environmental variables. The intertidal

habitats located at Roebuck Bay, which contain a rich and abundant benthic invertebrate fauna may be more productive than at other locations (Pepping, 1999). Conversely, the increased growth of early age classes at Roebuck Bay may be a compensatory response to fishing pressure at this location reflecting a reduction in competition for food resources arising from low stock levels (Rochet, 1998; Hutchins, 2002; Winemiller, 2005). Such a conclusion, which implies that growth is density dependent, is consistent with the view that Roebuck Bay has a long history of commercial, recreational and indigenous fishing pressure (Morrissey, 1985), whereas, for example, *P. macrochir* have only been targeted at Anna Plains since *ca* 1996.

The parameter estimates for the von Bertalanffy growth curve for *P. macrochir* derived during this study are the first presented for this species and this function fitted the length at age data for this species in north-western Australia very well. Although Bibby & McPherson (1997) fitted a Schnute growth curve to length at age data for *P. macrochir* from the Gulf of Carpentaria, the curve had a relatively poor fit and no conversion was attempted enabling an estimate of L_∞ to be derived. The maximum total length recorded for *P. macrochir* during this study, *i.e.* 1393 mm, is smaller than that recorded elsewhere in Australia waters, *i.e. ca* 1450-1625 mm **(Table 6.5)**. Furthermore, the maximum age of *ca* 10 years is considerably smaller than those recorded for this species by other workers **(Table 6.5)**. For example, some individuals of *P. macrochir* from the Fitzroy River region in southern Queensland live to an age of *ca* 19 years (Halliday *et al*., submitted). The marked disparity in the age composition between north-western Australia and southern Queensland presumably reflects differences in fishing mortality between the two regions and suggests that north-western Australian populations may be more heavily exploited than the southern Queensland population studied by Halliday *et al*. (submitted). The maximum weights of *P. macrochir* caught during this study are very similar to recreational angling records for this species, *i.e. ca* 16 kg (Anon, 2006a). Although commercial fishers in north-western Australia have, on occasion, caught *P. macrochir* individuals weighing *ca* 20 kg, there appears to be no evidence that this species attains the >45 kg reported anecdotally (*e.g.* Stead, 1906).

6.4.2. Mortality and yield and spawning biomass per recruit

The far greater growth coefficient, *k*, and smaller asymptotic length recorded for *E. tetradactylum* than *P. macrochir* would be expected to be accompanied by a higher rate of natural mortality, *M* (*e.g.* Beverton and Holt, 1957; Pauly, 1980). This prediction is borne out by the greater values derived for *M* for *E. tetradactylum* using both the refitted equation of Pauly (1980) and the Bayesian approach of Hall *et al.* (2004), *i.e.* 0.68 and 0.61 $year^{-1}$, respectively, than those derived for *P. macrochir* using the same methods, *i.e.* 0.35 and 0.31 $year^{-1}$, respectively. These comparisons imply that the stock of *E. tetradactylum* is more productive and more likely to sustain exploitation than those of *P. macrochir*. Although the estimate of fishing mortality, *F*, was similar to that for *M* for *E. tetradactylum*, the estimate of *F* for *P. macrochir* greatly exceeded that of *M*. As it is generally regarded favourable if an exploited stocks fishing mortality rate does not exceed the rate of natural mortality for that stock (Gulland, 1983), the above findings suggest that *E. tetradactylum* is fully-exploited and that *P. macrochir* is subject to overfishing.

In the context of *P. macrochir*, it may thus be relevant that commercial fishing for threadfin species in north-western Australia is now focused mainly on this larger species. Furthermore, the estimate of *F* derived for *P. macrochir* during this study may actually underestimate the true rate of fishing mortality experienced by this species in north-western Australia. The basis for this conclusion is that the estimate for total mortality (*Z*), derived for this species used recreational tagging data largely collected from the Dampier region of north-western Australia, a location outside the bounds of the main commercial fishery for this species and thus presumably represents a less exploited stock than at either Roebuck Bay or Anna Plains. The extremely high values for *F* derived for another species of threadfin *Polydactylus mullani* in India (Prasad *et al*., 2005) provide strong indications that such species are highly vulnerable to fishing.

The view that *P. macrochir* is subject to overfishing and that *E. tetradactylum* is also relatively heavily fished is supported by the fact that the current estimates for *F* for both species exceed those for the $F_{0.1}$ reference points for those species (Hilborn & Walters, 1992; Haddon, 2001). The yield per recruit analysis also indicates that the age at recruitment of both threadfin species to the fishery has an important influence on the potential yield. Thus, if the ages at recruitment to the fisheries for *E. tetradactylum* or

P. macrochir were to be reduced by only one year, the yield of particularly the former species would be substantially reduced.

A marked reduction in spawning stock biomass could lead to recruitment overfishing. In this context, the more dramatic declines in the spawning potential ratios of the females than males of *E. tetradactylum* and *P. macrochir* as fishing mortality increases from 0 to 1.5 year^{-1} demonstrate that, for these hermaphroditic species, it is critically important to take into account the lengths over which individuals change sex. At the current estimated level of fishing mortality of 0.45 year^{-1} for *P. macrochir*, the SPR of the females of this species at Roebuck Bay and Anna Plains are predicted to have declined to 0.13 and 0.16, respectively, which are well below the limit reference point of 0.3, *i.e.* 30% of mature female virgin stock biomass. This strongly indicates that both stocks of this species are overfished and thus *P. macrochir* is at a high risk of recruitment failure (Mace & Sissenwine, 1993).

In the case of the females of *E. tetradactylum*, the point estimate of 0.36 for the current level of SPR is approaching the 0.3 reference point. Thus, the SPR of this latter species requires monitoring to ensure that it does not decline beyond the limit reference point of 0.3. The age at recruitment of *E. tetradactylum* to the exploited stock has important consequences for its management. For example, if this age was to be reduced by one year to age 1, the SPR of the stock at the current estimated level of *F* would lie well below the 0.3 reference point. In this respect, it is important to recognise that a considerable number of *E. tetradactylum* are currently caught at 1 year of age. Thus, further increases in the capture and retention of this age class should be avoided.

The management implications of the results presented in this chapter are discussed further in Chapter 7.2.

7. Conclusions

7.1. Use of nearshore waters by fish

The fish catches from nearshore waters at all three sampling locations along the Canning coast, *i.e.* Port Smith, Eighty Mile Beach and Cape Keraudren, collectively yielded 170 species representing 66 families. The majority of species have an Indo-Pacific distribution and the overall species composition was similar to that observed in other shallow coastal waters in northern Australia (*e.g.* Blaber & Blaber, 1980; Rainer & Munro, 1982; Rainer, 1984; Blaber *et al*., 1990; 1994, 1995). However, the ichthyofauna of the arid Canning coast differs from that in other parts of tropical Australia in that it contains at best low contributions of those taxa which are typically associated with reduced salinities, such as *Toxotes*, *Ophiocara, Zenarchopterus* and *Pseudomugil.* In this respect, the fauna of the Canning coast is similar to that recorded by Blaber *et al*. (1985) for Dampier, which is located *ca* 300 km to the south on the Pilbara coast and also receives very little fresh water input.

Blaber *et al*. (1985) noted that the fish fauna inhabiting the clear waters of Dampier differed from that of other Indo-Pacific coastal waters in that turbid water taxa, such as members of the Sciaenidae, Engraulidae, Polynemidae and Cynoglossidae, were poorly represented. In this respect the fauna of nearshore waters along the Canning coast is intermediate between Dampier and other coastal waters of the Indo-Pacific and thus presumably represents a transitional fauna. For example, all of the above mentioned taxa were caught at Eighty Mile Beach, which was the most exposed sampling location, characterised by fine sediments and turbid waters. In contrast, the protected nearshore waters at Port Smith were relatively clear and the fish fauna at that location was very similar to that found at Dampier, with low contributions made by species typically associated with turbid waters. It is thus relevant that turbidity was more influential in structuring the fish communities at the three locations along the Canning coast than factors associated with latitude.

The ichthyofaunas At Port Smith and Cape Keraudren were also influenced by the habitat types found at these locations. The use of rotenone in intertidal pools and seine

netting in adjacent shallow, nearshore waters demonstrated that there is very little overlap in the species found in the two habitats and that the fauna of intertidal pools was strongly influenced by the presence of rock or mangroves. Gill netting in both unvegetated waters and in mangroves illustrated that the fish communities found in these two habitats differ, reflecting the consistent tidal migrations made by different species into the two habitats. The consistency of the differences in species composition is marked considering the very large tides of the Canning coast mean that these intertidal habitats are only temporarily available to fish for a few hours at a time.

Fifty three of the species caught are fished commercially and recreationally along the Canning coast and a further 17 fish species are caught solely by recreational fishers. The most abundant of these species were the polynemids *Eleutheronema tetradactylum* and *Polydactylus macrochir*, which are residents of nearshore waters, *i.e.* they are found in these waters throughout the whole of their life cycle. Other species, such as *Lutjanus russelli, Epinephelus coioides* and *Sillago vittata,* are present in nearshore waters only as juveniles and thus use these waters as a nursery area. The nursery role of nearshore waters is illustrated by the way in which the species compositions of the samples caught with the seine net in shallow, nearshore waters and with rotenone in intertidal pools underwent a cyclical progression during the year, reflecting the timing and strength of recruitment of the juveniles of the various species. In addition, nearshore waters also acted as a nursery area for a number of elasmobranchs during the wet season, including the endangered Green Sawfish *Pristis zijsron.*

The majority of the species that use nearshore waters as a nursery area along the Canning coast also employ such waters as a nursery in other regions. For example, although *E. tetradactylum* frequently occurs in estuaries, this species predominantly uses shallow inshore coastal waters as a nursery area (Shubnikov, 1978; Blaber & Blaber, 1980). In contrast, other species, such as *Craterocephalus mugiloidies, Craterocephalus capreoli* and *Platycephalus endrachtensis,* which also occur in south-western Australia, are largely restricted to estuarine environments in the latter region. The use of alternative habitats by the juveniles of these species demonstrates the opportunistic nature of these species and illustrates the importance that nearshore waters play as a nursery area in those

regions where there are no estuaries (Lenanton & Potter, 1987).

Recent fish and fish habitat conservation efforts in Australia have concentrated on temperate and sub-tropical regions, where the fish fauna is characterised by high levels of endemism and the number of species offered protection can be maximised (Pogonoski *et al*., 2000; Fox & Beckley, 2005). However, while endemism in nearshore waters of northern Australia is less than in southern Australia, reflecting the fact that most species also occur throughout the Indo-Pacific, the conservation value of these species is still high as the habitats of these species in other parts of their range are at high risk (Blaber, 2000; Pogonoski *et al*., 2000). Thus, the data on the diversity, abundance and species compositions of fish faunas in different nearshore habitats along the Canning coast of north-western Australia, and the way these faunas are influenced by season, provides fisheries and environmental managers with information that will assist them to develop effective management plans for these habitats and their fish species.

7.2. Biology of *Eleutheronema tetradactylum* and *Polydactylus macrochir* and implications for management

Analysis of length and age compositions of the different sexes of *Eleutheronema tetradactylum* and *Polydactylus macrochir* and an examination of the histological characteristics of the gonads of the full size range of threadfin demonstrated that, in north-western Australian waters, both of these species are protandrous hermaphrodites. Threadfin species are highly regarded for their eating qualities and form the basis of important commercial, recreational and subsistence fisheries around the world. However, in recent years, the yields of some threadfin species have undergone an alarming decline (*i.e.* Abohweyere, 1989; Szyper *et al*., 1991; Cheung & Sadovy, 2004; Kizhakudan & Kizhakudan, 2005). In certain cases, the declines have been attributed to the failure of managers to appreciate the need to understand the consequences of fishing protandrous hermaphrodites (Bensam & Menon, 1994; Friedlander & Ziemann, 2003; Poepoe *et al*., 2003).

The structure of the bisexual gonads of *E. tetradactylum* and *P. macrochir* and the pathway for protandrous sex change in these two species is very similar. Despite their

overall similarities, the timing of sex change by these two polynemids differs markedly. For example, in the majority of *E. tetradactylum,* sex change occurs during the second or third years of life, whereas sex change takes place in *P. macrochir* at any time between their second and seventh years. The large difference in the ages and lengths at which these species change sex presumably reflects the fact that *P. macrochir* lives longer and grows far larger than *E. tetradactylum*, *i.e.* 1393 mm and 10 years *vs* 793 mm and 6 years, respectively. The age and length at which *P. macrochir* changed sex differed among locations. In contrast, *E. tetradactylum* changed sex at similar ages and lengths at all locations. The differences in the biology of the two threadfin species need to be taken into account when developing management plans for these species.

Despite declines in the catches of some threadfin species, few attempts have been made to carry out stock assessments on polynemid species. Furthermore, no stock assessment has taken into account that these species are protandrous, presumably because it is more difficult to develop reliable per-recruit models for hermaphroditic than gonochoristic species as it requires a thorough understanding of the length and age at which sex change occurs (*e.g.* Buxton, 1992; Punt *et al.*, 1993; Huntsman & Schaaf, 1994; Hesp *et al*., 2004; Heppell *et al*., 2006). The biomass-per-recruit analysis undertaken on *E. tetradactylum* and *P. macrochir*, which incorporated the sizes and ages at which these species change sex, represents the only such analysis yet reported for a polynemid. The resulting analyses demonstrated that the stock *E. tetradactylum* in north-western Australia appears to be fully exploited and that the stock of *P. macrochir* is subjected to overfishing, *i.e.* experiencing fishing mortality in excess of that which would ensure that the reproductive potential of the stock is sustained at an adequate level.

At a broader level, the per-recruit analyses serve to illustrate the alarming ease with which the female spawning biomass can become eroded in protandrous fishes which are subjected to high fishing pressure. Protandry has evolved repeatedly across a wide range of phyla reflecting the relatively high reproductive success afforded to females at a large size, particularly in terms of fecundity. Thus, the vulnerability of protandrous species lies in the fact that, as fishing frequently targets the upper length and age classes, *i.e.* highly fecund females, which have already been reduced in numbers by the cumulative

impact of fishing mortality on younger age classes, even relatively low exploitation rates are likely to have an adverse affect on the total egg production of a population.

The very marked decline in female biomass with increasing fishing pressure, that is predicted by models of the stocks of *P. macrochir* in north-western Australia, parallels the situation observed with the protandrous barramundi *Lates calcarifer* in Queensland, where the number and maximum size of mature females is far lower in rivers that are heavily fished than in those that are closed to fishing (Halliday *et al*., 2001). Ley & Halliday (2004) estimated that the total egg production of *L. calcarifer* in rivers closed to fishing may be 20 times greater than that in heavily-fished rivers. The reduced egg production, which reflects the loss of spawning stock, has adversely affected the recruitment of this species with the number of small *L. calcarifer* being much lower in rivers open to fishing than those closed to fishing (Ley *et al*., 2002).

The sustainable management of *P. macrochir*, as with *L. calcarifer*, requires actions that will ensure that egg production is conserved through the protection of female biomass, thus guarding against recruitment overfishing. The present minimum legal length (MML) of 450 mm for *P. macrochir* in north-western Australian waters is well below the length at which this species typically changes sex in this region (L_{50} at sex change = 793-1158 mm) and thus fails to protect females from capture. Although the MLL could be increased to a length that would increase the proportion of males that become females and would protect some females, such a move should take into account the fact that most of the catch of *P. macrochir* is taken by commercial gill net fishers, and that few threadfin survive capture by gill nets. Thus, an increase in the MLL on its own would not be an effective way to facilitate the conservation of the stocks of this species.

Changes in the mesh size of commercial gill nets would need to be implemented to effect a change in the size of fish caught. At present, the gill net fishery targeting *P. macrochir* is essentially a gauntlet fishery in that the majority of egg production presumably comes from the small component of females, which have grown to a size larger than that selected by the gill nets in use. Milton *et al*. (1998) suggested that a reduction in mesh size would protect the largest and most fecund *L. calcarifer* in Papua New Guinea and such a move might serve to protect the female biomass of *P. macrochir*

in north-western Australia. However, as pointed out by Fonseca *et al*. (2005), when contemplating a mesh size change in a multi-species fishery, the consequences for each species needs careful consideration. In a gauntlet fishery for a protandrous species, it is essential to ensure that a decrease in mesh size does not impact negatively on reproductive output by reducing the proportion of fish that survive to become females. Furthermore, it is important to remember that yields cannot be maximised for all the species in a multi-species fishery (Maunder, 2002).

Although *P. macrochir* makes the largest contribution to the Kimberley Gill net and Barramundi Managed Fishery (*ca* 60% by weight), this fishery is largely managed with the aim of conserving the stocks of Barramundi. Thus, fishers are already restricted by a closed fishing season during December and January, which is reported to be the peak spawning period for *L. calcarifer* in northern Australia. Although *P. macrochir* also spawns in north-western Australia during those months, peak spawning starts about one month earlier and the inclusion of November in the period closed to fishing may offer *P. macrochir* an additional measure of protection.

Although per-recruit analyses suggest that *E. tetradactylum* is not currently subject to overfishing, this species appears to be fully exploited and its stocks need to be monitored to ensure that overfishing does not occur in the future. The potential susceptibility of this species to increases in fishing pressure is highlighted by the situation with the Moi *Polydactylus sexfilis* in Hawaii, which is biologically very similar to *E. tetradactylum*. Failure to appreciate that *P. sexfilis* was protandrous led to a high level of exploitation of this stock resulting in a drastic decline in catches and ultimately in recruitment failure (Szyper *et al*., 1991; Friedlander & Ziemann, 2003). As the data for *E. tetradactylum* demonstrate that recreational fishers currently retain appreciable numbers of fish with lengths below that at which this species changes from male to female (L_{50} at sex change = 397 mm, Chapter 5), managers and stakeholders need to consider introducing a legal length for retention that takes into account this length at sex change. Such a management measure would be appropriate as *E. tetradactylum* is caught mainly by recreational fishers and would be likely to survive release following their capture by rod and line.

In view of the confusion that persists regarding the identification of *E. tetradactylum* and *P. macrochir* by recreational fishers, an attempt to enforce different size and bag regulations for these two species would likely be ineffective. Since the recently introduced MLL of 450 mm for *P. macrochir* did not take into account crucial details of the biology of that species, it offers little protection. It might thus be appropriate to introduce a MML of 400 mm for both species. Such a measure should not adversely affect *P. macrochir* as that species is caught mainly by commercial fishers at much larger lengths. Furthermore, since considerable numbers of 0+ and 1+ *E. tetradactylum* are currently retained by recreational fishers, the introduction of a MLL of *ca* 400 mm for this species in north-western Australia would increase the age of recruitment to *ca* 2 years. Although the per-recruit analyses suggest that, while such a measure would greatly reduce the chance of recruitment over-fishing by ensuring that a large component of the stocks of were able to change sex to become female prior to capture, it is unlikely that yields will be adversely affected.

From a management point of view, it is also important to recognise that the two threadfin species in north-western Australia are restricted to nearshore waters and are therefore easily targeted by fishers. Thus, the creation of MPAs in north-western Australia could prove a valuable management initiative for sustaining the stocks of *E. tetradactylum* and *P. macrochir*. It is likely that MPAs would conserve the age structure of these two species (e.g. Berkeley *et al*., 2004) and provide protection for female biomass, egg production and recruitment of these threadfin species as they do for the protandrous *L. calcarifer* (Ley & Halliday, 2004). In addition, as outlined above, the implementation of MPAs in nearshore waters would have the added benefit of conserving other species which use the same habitats, either as a nursery area or throughout their life, but for which data may be deficient (Johannes, 1998). The biological data produced for *E. tetradactylum* and *P. macrochir*, and the results of the stock assessments performed on these species, will enable fisheries managers to develop effective management plans for conserving the stocks of these two species in north-western Australia.

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